RESOURCE COMPETITION, SPACE USE AND FORAGE ECOLOGY OF SEA OTTERS, *ENHYDRA LUTRIS,* IN SOUTHERN SOUTHEAST ALASKA

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A

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Abstract

The growing sea otter population in southern Southeast Alaska is impacting commercial shellfish, through foraging and expanding in range and abundance except where hunted for subsistence. Sea otters and their prey have coexisted in the North Pacific Ocean for approximately 750,000 years, but due to exploitation of sea otters from the 1770s until 1911, the species became extinct over much of its range, including southern Southeast Alaska. Subsequently, invertebrate species flourished and were commercially targeted in the late 1900s. Sea otters were relocated (n = 106) to southern Southeast Alaska in 1968. In this dissertation, I evaluated this marine mammal-fisheries conflict through multiple approaches. In Chapter 1, I analyzed geoduck clam and red sea urchin abundance surveys (1994-2012) and catch and effort data from commercial Dungeness crab fisheries (1969-2010) to identify interactions between sea otters and commercial shellfish. In Chapter 2, I collected geo-locations from 30 instrumented sea otters (2011-2014) to identify space use and range expansion. In Chapter 3, I collected sea otter abundance and distribution data from fixed wing aircraft (2010-2014) and observational forage data from sea otters (2010-2013) to determine contemporary population growth and consumption of commercially important shellfish by sea otters. The sea otter population in southern Southeast Alaska has grown from 106 to an estimated 13,139 individuals between 1968 and 2011 with an annual growth rate of 12% and expansion of its range by 117 $km^2 y^{-1}$. Results from a before-after, control-impact analysis indicate that sea otters are rapidly impacting red sea urchin and significantly reducing geoduck clam densities. Further, breakpoints predicted from regression models of Dungeness crab catch are correlated with known sea otter colonization timing. Forty-six percent of the population level diet of sea otters represented commercially important prey. Sea otters targeted commercially important species, specifically red sea urchins and Dungeness

crab, when first colonizing an area, after which the diet of sea otters became more diverse as colonization durations increased. Using habitat models based on a bivariate normal probability distribution function, environmental covariates and subsistence hunting pressure on sea otters, I determined that sea otter range expansion was limited by subsistence hunting. Further, female and non-territorial males segregated based on habitat and likely prey preferences. I conclude that sea otter populations will likely continue to grow, and that current shellfisheries cannot coexist with sea otters under existing management. Further, conservation and management of sea otter populations, whether to increase the distribution through translocation efforts or reduce the distribution to avoid human conflicts, could benefit from insights gained from spatially explicit modeling at the landscape level.

Table of Contents

List of Figures

List of Tables

List of Appendices

Dedication and Acknowledgments

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General Introduction

Sea otter biology and ecology

Sea otters (*Enhydra lutris*) are the largest member of the weasel family, the smallest marine mammal, and possesses many characteristics which have allowed them to evolve in the North Pacific (Jefferson et al. 1993). Though the species has adapted to temperate waters, they have little subcutaneous fat (Kenyon 1969). Instead sea otters depend on dense water-resistant fur to provide insulation from cold waters (Williams et al. 1992). This fur has been highly sought after for clothing and fashion since at least 1742 (Kenyon 1969). The fur is the thickest known mammal fur, with as many as 164,662 hairs cm^{-2} (Williams et al. 1988). Because of their small body size and lack of blubber, sea otters compensate by maintaining a high level of internal heat production, which requires high standard metabolic rates. Captive sea otters have been observed to consume 189-253 kcal kg^{-1} daily to compensate (Costa and Kooyman 1982, Kenyon 1969). Their assimilation efficiency is 80%-85% which is low compared to most marine mammals. The basal metabolic rate of sea otters is 8 times the basal metabolic rate of a terrestrial mammal of equal size (Costa 1982, Costa and Kooyman 1984).

The ecology of sea otters has been well studied. Sea otters are keystone species and have large impacts on coastal ecosystems using top-down control (Estes and Palmisano 1974, Hughes et al. 2013, Power 1992, Power et al. 1996). Further, sea otters inhabit shallow coastal water and are typically distributed in areas in which bathymetry allows them to effectively forage on benthic invertebrates. The maximum dive depth of sea otters is approximately 100 m and sea otters

typically forage in water < 60 m in depth (Bodkin et al. 2004, Newby 1975). The benthic habitat types which sea otters occupy and prey types which they consume vary throughout their range (Newsome et al. 2015, Riedman and Estes 1990). The species forages in both the intertidal and subtidal and at both night and day (Esslinger et al. 2014, Weitzman 2013). Sea otters capture prey with their forepaws and often store food items within skin folds underneath their forelegs (Riedman and Estes 1990). Prey item are brought to the surface and consumed (Tinker et al. 2008a). Tool use is common and occasionally sea otters will steal food from one another (Kenyon 1969).

Population growth in sea otters is limited by both physiological and environmental constraints. In areas where sea otters are not resource limited, the reproductive cycle of a female is approximately one year and the theoretical maximum annual growth rate of a population is estimated to be 20% (Estes 1990). Mating and pupping can occur throughout the year, with seasonal peaks being observed in some populations (Garshelis et al. 1984, Kenyon 1969). Sea otters are polygamous and females reach sexual maturity between 3 and 5 years of age, while males reach competitive maturity at approximately 7-8 years of age (Riedman and Estes 1990). Further, females can come into estrus and mate within a few days of weaning a pup (Garshelis et al. 1984). Like all marine mammals sea otters give birth to a single offspring (Jefferson et al. 1993). Gestation periods have been measured from 5 to 9 months, and this variability is likely due to the ability to delay implantation (Sinha et al. 1966).

A final aspect of sea otter ecology important to the themes presented within this dissertation is the relative sedentary nature of sea otters compared to other marine mammals. Sea otters do not

migrate seasonally and have small home ranges (Garshelis and Garshelis 1984, Jameson 1989, Loughlin 1980, Ralls et al. 1996). In a remnant population in California, southward range expansion was estimated at 5.2 km y^{-1} and 95% of movements were < 23 km y^{-1} (Tinker et al. 2008b). In a reintroduced population in Washington, from 1992-1999, females used an average of 24 km of coastline, and range expansion was minimal despite population growth rate of 8% (Laidre et al. 2009). Even when large movements have been observed, sea otters will generally return to areas known to them (Jameson 1989).

Sea otter history and demographics in Southeast Alaska

Sea otter populations have experienced many conservation challenges in Alaska. As a result of the fur trade of the 18th and 19th century, sea otters persisted at only five isolated locations in Alaska, none of which existed south of Prince William Sound (Kenyon 1969). In 1911 sea otters were protected internationally as part of the Fur Seal Treaty of 1911, which placed a moratorium on the take of sea otters (Elliott and Hay 1911). Sea otter populations were managed by the United States Fish and Wildlife Service (USFWS) beginning in 1940, and in the 1950s the agency began translocation efforts from sea otters at Amchitka Island to the Pribilof Islands and Attu Island (Kenyon and Spencer 1960). The state of Alaska gained management authority of sea otters in 1959, when statehood was granted, and the Alaska Department of Fish and Game (ADF&G) began extensive transplants in cooperation with the Atomic Energy Commission (Jameson et al. 1982). In 1965 sea otters were translocated to Yakutat Bay and Khaz Bay in Southeast Alaska and translocations continued at five other locations in Southeast Alaska between 1966-1969 (n = 413 sea otters, Burris and McKnight 1973) . The reason for the reintroduction was in part to provide for a renewed sea otter fur industry and in part to mitigate

the impact of underground nuclear testing by the United States Atomic Energy Commission (VanBlaricom 2015). In 1968, 1000 sea otters were harvested from remnant populations, and the pelts were auctioned by the state of Alaska, the first since the moratorium on harvest in 1911 (Burris and McKnight 1973, Kenyon 1969). On Oct. 21, 1972 the enactment of the Marine Mammal Protection Act (MMPA) brought management authority for sea otters back to the federal government (USFWS; Marine Mammal Protection Act 1972). No further sea otter translocations occurred from Alaskan sea otter populations, and the prospect of a sea otter fur industry was abandoned (Johnson 1982). The MMPA renewed the moratorium on harvest of sea otters, with the exception of coastal Alaska Natives. Harvest, allowed under an exemption of the MMPA, was limited to prevent industrial harvest of sea otters while allowing for Alaska Natives to continue with traditional uses of sea otters. Although poorly defined, sea otter pelts must be incorporated into a "handicraft" before being sold, making the sale of raw pelts illegal (Marine Mammal Protection Act 1972).

All translocations to Southeast Alaska were successful, and the population has grown to approximately 25,000 sea otters in 2012 (USFWS 2014). This conservation success story is not viewed positively by a large segment of Southeast Alaska residents. Sea otters have ecologically and economically significant effects on coastal ecosystems of the North Pacific Rim, as a result of their foraging activities and preferences (VanBlaricom and Chambers 2003). In the absence of sea otter predators, the nearshore community structure shifted, macroinvertebrates biomass increased and commercial shellfisheries developed (Estes and VanBlaricom 1985). It is likely that several of the existing commercial shellfisheries could not have existed without the extirpation of sea otters (Bodkin et al. 2004). Sea otters began competing with commercial

fisheries managed by the ADF&G, by the 1980s, and due to protection by the MMPA, animosity toward sea otters and management agencies began (Johnson 1982). Animosity continued through the 1990s as the sea otter population continued to grow and the harvest by coastal Alaska Natives remained low (R. B. Benter, USFWS Marking Tagging Reporting Program, personal communication 2014, USFWS 2014). This animosity intensified through the 2000s (Carswell et al. 2015). Hunting pressure by coastal Alaska Natives intensified in the 2010s (R. B. Benter, USFWS Marking Tagging Reporting Program, personal communication 2014). Since 1993, the ADF&G has closed at least 18 dive fishing districts in Southeast Alaska, due to low resource abundance from presumed sea otter predation in combination with commercial fishing (Hebert 2014). Further, over the last 30 years the spatial distribution of Dungeness crab (*Metacarcinus magister*) catch appears to have been impacted by competition from sea otter populations; however, the link between sea otters and the reduction in commercial fisheries was largely based on anecdotal information. (Esslinger and Bodkin 2009, Larson et al. 2013, USFWS 2014). No studies have examined the interaction of sea otters with commercial fisheries or fished species in Southeast Alaska, with the exception of a companion study by Larson et al. (2013) and further minimal effort had been made to correlate demography and diet of sea otters in the region (Esslinger and Bodkin 2009, Kvitek et al. 1993).

As tensions grew due to increased sea otter abundance and distribution, the ability for Alaskan Natives to market products made from sea otter pelts was limited (Didrickson v. U.S. Dept. of the Interior, 1991). Although court decisions provided some clarity regarding which products could be made from sea otters, fear of enforcement action for selling items defined by ambiguous terms limited the harvest of sea otters in the 1990s (Carswell et al. 2015). Several undercover

operations ended up prosecuting costal Alaska Natives in mid-2000s for violation of the MMPA (Carswell et al. 2015). In the mid-2000s I heard anecdotal reports of sea otters being taken by commercial dive fisherman while fishing in remote and unpatrolled areas of southern Southeast Alaska. In 2004, I began recording sea otter presence while conducting SCUBA surveys for geoduck clams (*Panopea generosa*), sea cucumbers (*Parastichopus californicus)*, red sea urchins *(Strongylocentrotus franciscanus)* and Pacific herring (*Clupea pallasii*) while I was employed by the ADF&G. By 2007 it was clear sea otter distribution overlapped with much of the commercial biomass for these commercially important prey species and I observed evidence of sea otter predation on SCUBA transects (Pritchett and Hoyt 2008). In 2010 the fishing industry lobbied both state and federal legislators from Alaska to liberalize harvest regulations and allow coastal Native Alaskans to more easily harvest sea otters to reduce competition with commercial fisheries (Carswell et al. 2015). Concurrently, I began conducting research that led to this dissertation with colleagues from the USFWS and University of Alaska Fairbanks and with input from the ADF&G, fisheries stakeholders and ecotourism operators. Although legislative changes did not occur, the public opinion of sea otters motivated indirect funding from the state of Alaska for the purchase of sea otter pelts from subsistence hunters to encourage and teach sewing practices through the Sealaska Heritage Institute (Sealaska Heritage 2013). The continued increase in sea otter numbers, indirect economic incentives, public perspective, and outreach on clarifications by the USFWS regarding sea otter harvest regulations increased the number of sea otters taken to a record 1495 individuals in 2013, far greater than the prior 10 year (2003-2012) average of 496 individuals (± 223.3 *SD*) in Southeast Alaska (R. B. Benter, USFWS Marking Tagging Reporting Program, personal communication 2014).

Purpose and organization of dissertation

The rate at which sea otters have and will continue to recolonize Southeast Alaska is of great importance to the commercial Dungeness crab and dive fishing fleets, sport and subsistence fishermen, including sea otter harvesters, and the coastal communities of the region. Abundance and distribution surveys conducted since 1975 have provided some insight into the rate of sea otter colonization; however, surveys have not been conducted regularly, and no known studies on movement, colonization or habitat use have occurred in the region. Sea otter populations are impacted by several factors, including predation, hunting, resource limitation, pollution and disease (Ballachey et al. 2003, Bodkin and Ballachey 2010, Bodkin et al. 2011, Estes et al. 2005, Estes et al. 1998, Ostfeld 1982). However, which, if any, of these mechanisms are impacting sea otters is unknown in southern Southeast Alaska.

Within this dissertation I evaluated if sea otters are directly impacting commercial fisheries using both fisheries dependent and independent data collected by the ADF&G, sea otter survey data collected from 1975 to 2014, and sea otter forage data collected from 2010-2013. In addition, I characterized sea otter space use using telemetry data. The dissertation has three distinct chapters. Chapter 1 represents a comprehensive analysis of the direct impact of sea otters on three commercially important shellfish, including Dungeness crab, geoduck clams and red sea urchins. The analyses correlate reductions in biomass and catch of shellfish to sea otter presence. In chapter 2, I determined if sea otters colonized new areas, what limitations existed to population growth and distribution and identified variables important to habitat selection of sea otters at a frontal boundary of the population. This was accomplished using a habitat model

based on telemetry data from 30 sea otters collected near Kake, Alaska in conjunction with environmental and subsistence hunting covariates. The objectives of this chapter were to determine if sea otters were recolonizing unexploited habitat and if certain habitat types were selected or avoided by sea otters. Additionally, I examined if limitations to sea otter population growth existed in the region. Chapter 3 focuses on the diet of sea otters as a function of recolonization, abundance, and distribution, using a space-for-time structured analysis. Specifically, I determined the association of variables including persistence (duration of sea otter occupation), sea otter density, exposure to the Gulf of Alaska, and distance from release site with the diet of sea otters in southern Southeast Alaska. To summarize, I determined: 1) if sea otters are impacting commercial fisheries, 2) if sea otters area colonizing new areas or if limitations exist, and 3) the diet composition of sea otters as it relates to commercially important prey species and sea otter recolonization. The goal of this dissertation is to provide scientifically grounded information to inform the conflict between sea otters and resources users, where limited or anecdotal information previously existed. This dissertation is prepared for submission to three ecological journals specified in the footnote of each chapter title page. Each manuscript includes multiple authors. I am the first author on all manuscripts presented and contributed most to the project development, organized and participated in all data collection, analysis and manuscript preparation. Co-authors participated, to a lesser degree, in project development including grant writing, data collection, and providing comments, which improved writing and analyses.

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Chapter 1: Reductions in commercially important macroinvertebrates associated with sea otters (*Enhydra lutris)* in Southeast Alaska[1]

Abstract

Marine mammal-fisheries interactions are a global conservation challenge that is difficult to quantify. Recovery of sea otters (*Enhydra lutris)* in Southeast Alaska after extirpation in the fur trade (1741-1911) provides an example of a marine mammal fishery interaction where fisheries are rapidly and dramatically declining while the marine mammal thrives. The absence of sea otters in Southeast Alaska (1850s-1968) allowed invertebrate prey species to flourish and commercial fisheries to develop (1970s-2000s). Before-after control-impact analyses of fishery-independent surveys for red sea urchin *(Strongylocentrotus franciscanus)* and geoduck clams (*Panopea generosa*) from 1994 to 2013 showed declines attributable to sea otters. Additionally breakpoint analyses of Dungeness crab (*Metacarcinus magister*) catch records from 1969-2010 revealed breakpoints corresponding with sea otter colonization timing. Sea otter presence dramatically diminished red sea urchin density and Dungeness crab catch within 5 years of colonization, while geoduck clam density decreased more gradually over a longer (~4-12 year) cumulative presence of sea otters. The sustainability of shellfish fisheries is questionable in the presence of this apex predator.

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Introduction

Marine mammals impact commercial fisheries throughout the world, and the topic has gained growing attention in the last 15 years (Mackinson et al. 2003, Morissette et al. 2012, Yodzis 1998). Marine mammal fisheries interactions can be either direct or indirect. Direct interactions with fisheries occur when marine mammals interact with fishing gear (Purves et al. 2004). For example, killer whales (*Orcinus orca*) depredate longline fishing gear throughout the world, causing loss to catches and fishermen's income (Garrison 2007, Hamer et al. 2012). Indirect interactions occur when marine mammals forage on commercially important species or on other key species in trophic food webs. Indirect interactions are often difficult to assess, because fisheries independent data are difficult and costly to obtain (Pennington and Strømme 1998), and empirical evidence linking marine mammal populations with trends in fish abundance rely on unrealistic assumptions or are lacking altogether (Plaganyi and Butterworth 2005, Trites et al. 1997). An example of an indirect interaction of a marine mammal on a commercial fishery is predation on hakes (*Merlussius spp.*) by Cape fur seals (*Arctocephalus pusillus)* off of South Africa (Punt and Butterworth 1995). Extensive harvest of fur seals for their furs during colonial times reduced their population, which subsequently increased through marine mammal conservation efforts. Their impact to fisheries is difficult to quantify, as fur seals forage nocturnally in deep water (up to 400 m) and consume their prey, which is mobile and patchy in distribution, below the surface (Wickens et al. 1992a). Fisherman claim that culling fur seals will increase fish stocks, and yet, mathematical models suggest that culling may actually cause reductions in the commercial catch of hake due to complexities in the marine food web (David and Wickens 2003, Wickens et al. 1992b).

The impact of sea otters on commercial fisheries may be quantified with fewer assumptions than for other marine mammals, as sea otters and their prey are distributed nearshore in shallow water and are relatively sedentary, and sea otters consume their prey at the surface and can be directly observed (Bodkin et al. 2004, Laidre et al. 2009). Sea otters have been implicated in causing large reductions in biomass and catch of commercial species, but limited empirical evidence is available (Estes and VanBlaricom 1985, Larson et al. 2013, Reidy 2011). Commercial sea cucumbers (*Parastichopus californicus)* represent approximately five percent of a sea otter's diet, and yet density of sea cucumbers was significantly reduced as sea otters recolonized Southeast Alaska, with 100% decline in areas occupied by sea otters since 1994 (Larson et al. 2013).

The impact of sea otters on abalone (*Haliotis spp.*) populations is difficult to disentangle from the effects of unsustainable fishing practices (Watson 2000, Woodby et al. 2005). Several species of abalone have been commercially harvested from California to Alaska over the last 125 years; however, only highly regulated recreational fisheries remain (Braje et al. 2013). Fanshawe et al. (2003) reported that sea otter predation restricted red abalone (*H. rufescens*) to densities and sizes inadequate to sustain a healthy fishery and concluded that marine reserves cannot serve as a tool for abalone fishery conservation in the presence of sea otters. Contrastingly, a positive relationship between sea otters and the endangered black abalone (*Haliotis cracherodii),* likely as a result of indirect effects, further informs the complexity of species interaction in the nearshore ecosystem but does not support the commercial potential of abalone in the presence of sea otters (Raimondi et al. in press). The conflict between sea otters, shellfish and humans is not

restricted to the modern day. Historical human control of sea otter populations through hunting may have been crucial to the development of a productive red abalone fishery in the California Channel Islands between about 7,300 and 3,000 years ago (Erlandson et al. 2005).

Sea otters may potentially impact geoduck clam (*Panopea generosa*) and Dungeness crab *(Metacarcinus magister)* fisheries because they eat both species, although the data on their impacts are very limited. Geoduck clams can burrow deep in the sediment, which may provide a refuge from sea otter predation and, therefore, sea otters may not impact the species when geoduck clams are abundant (Kvitek et al. 1992). In British Columbia commercial fishing effort was strongly associated with geoduck mortality and sea otters showed no significant effect on geoduck clam mortality; however, this study relied on unrealistic strong assumptions (Reidy 2011). Sea otters are implicated in the reduction in Dungeness crab fishing grounds in Prince William Sound and Southeast Alaska (Garshelis and Garshelis 1984, Shirley et al. 1996), but direct measurements of sea otter impacts on Dungeness crab are lacking. In eastern Prince William Sound, observations were made suggesting > 80% of the Dungeness crab standing stock was reduced as a result of sea otter colonization (Garshelis and Garshelis 1984, Garshelis et al. 1986). The Dungeness crab fishery was closed in Prince William sound in 1992 and no harvest has occurred since (Wessels et al. 2012).

Sea otters overlap with four commercial shellfisheries in Southeast Alaska, including red sea urchins *(Strongylocentrotus franciscanus),* Dungeness crab, sea cucumber and geoduck clams. These fisheries likely developed and flourished because of the absence of sea otters for over 100 years (Estes and VanBlaricom 1985, Katrina Wessels, USFWS, personal communication, 2014).

The 2013-14 ex-vessel value of these four fisheries was $16.9 million and has remained relatively stable (fifteen year average (1998-2013) = 14.8 ± 2.7 *SD* million dollars), while the catch has declined over the same period (Hebert 2014, Stratman et al. 2014). The majority of catch comes from the central and southern extent of Southeast Alaska (Hebert 2014, Stratman et al. 2014). The Dungeness crab fishery is the largest of the four fisheries in terms of both value and biomass harvested and is exploited using trap gear. The Dungeness crab fishery is managed by size, sex and season, where only males over > 165 mm carapace width are harvested during a set season, and early season harvest is used to set harvest duration (Stratman et al. 2014). Sea urchin, sea cucumber, and geoduck fisheries are prosecuted using SCUBA and managed using fisheries independent surveys to estimate a standing stock biomass and set a guideline harvest level (Hebert 2014, Larson et al. 2013).

The spatial and temporal distribution of sea otters in Southeast Alaska is important to understanding the conflict between sea otter and commercial shellfish fisheries. Sea otters were functionally extinct in Southeast Alaska by the mid-1800s as a result of the Russian, British and American fur trade, which began in the late 1700s and ended when an international moratorium on harvest was declared in 1911 (Kenyon 1969, Katrina Wessels, USFWS, personal communication, 2014). Subsequently, 106 sea otters were reintroduced to two locations in southern Southeast Alaska in 1968 (Burris and McKnight 1973). The sea otter population growth rate was estimated at 12% y^{-1} with a radial expansion of 1.42 km y^{-1} from introduction in 1968 to 2011, with the most recent stock assessment at 13,139 (cv = 0.17) individuals (USFWS 2014, Chapter 3). To date, sea otters have only recolonized 59% of the available habitat in southern Southeast Alaska. The contemporary distribution of sea otters provides an opportunity to conduct

a quasi-experimental approach to determine the indirect impacts of sea otters on commercial shellfisheries, where temporally and spatially structured fisheries data are available.

Sea otter populations have dramatic impacts on nearshore community structure due to metabolic demands and population dynamics. Sea otters are thought to forage optimally, and so their preferred prey is reduced rapidly (Ostfeld 1982). Red sea urchins are a preferred prey of sea otters where they coexist, and in southern Southeast Alaska sea otter prey intake rate was greatest when they preyed on red sea urchins (Laidre et al. 2009, Ostfeld 1982, Chapter 3). Sea otters are known to reduce the abundance and size of their prey, altering the nearshore community (Estes and Palmisano 1974, Hughes et al. 2013, Ostfeld 1982). The ability for sea otters to structure their environment is in part due to their high metabolic demand, as they do not have a blubber layer for energy storage or insulation, and consume up to 20% of their body weight daily (Costa and Kooyman 1982). Further, sea otter populations have a theoretical maximum growth rate of 24%, have high site fidelity, and do not migrate seasonally, which are characteristics known to cause rapid local reduction in the biomass of preferred prey species (Estes 1990, Garshelis and Garshelis 1984, Ralls et al. 1996, Chapter 2).

The objective of our study is to investigate the relationships between sea otters and commercial shellfish species in southern and central Southeast Alaska, as this region supports the largest proportion of nearshore shellfish fisheries in Alaska and is characterized by areas where sea otters are both present and absent. Specifically, we determine if sea otters are impacting red sea urchin and geoduck clam densities in areas where distributions overlap compared with areas where predator and prey have not contemporarily coexisted. Further, we determine if changes in

trends of Dungeness crab catch can be identified and, if so, determine if changes are associated with sea otter colonization in central Southeast Alaska.

Methods

Study area and species

The study area in central and southern Southeast Alaska includes two sea otter recolonization release sites and four commercial shellfish fisheries (Figure 1.1). We analyzed fisheries independent assessment data collected by the Alaska Department of Fish and Game (ADF&G) to assess geoduck clam and red sea urchin stocks in southern Southeast Alaska and fisheries catch data for Dungeness crab in central Southeast Alaska. We did not consider the impact of sea otters on sea cucumbers, as this was thoroughly investigated in a companion study (Larson et al. 2013), or on two other commercial species known to be prey of sea otters (red king crab, *Paralithodes camtschaticus,* and pinto abalone, *Haliotis kamtschatkana*), because they do not currently support commercial fisheries in our study area.

The spatial and temporal distribution of sea otters in the region was identified using survey and census data collected between 1975 - 2014 (Burris and McKnight 1973, Esslinger and Bodkin 2009, Hodges et al. 2008, Johnson et al. 1983, Pitcher 1989, Schneider 1975, USFWS 2014) and a GIS bathymetry coverage of potential sea otter habitat (area < 60 m in depth). Attributes derived from the contemporary distribution of sea otters used in analyses include the time since recolonization, i.e. sea otter persistence, and the least cost distance, i.e. as the sea otter swims,

from release site to the centroid of fishing districts, which was determined using ARCGIS 10.1 (ESRI 2012).

Red sea urchins

We analyzed survey data to determine if sea otters were impacting red sea urchins using a before-after control-impact (BACI) approach (Smith 2006), in which sea urchin density was surveyed at the same location (transect) over two time points (before and after) in areas with (impact) and without sea otters (control). Sea urchin density was surveyed by ADF&G SCUBA divers between 1994 and 2012 every three years at transects within the study area (Figure 1.2, Pritchett and Hoyt 2007). The number of red sea urchins counted along a 2 m wide transect located perpendicular to the shoreline within the 0 – 16.8 m depth range was divided by the total length of shoreline represented by a transect to obtain a linear density measurement (i.e. urchin per m shoreline), hereafter density (Pritchett and Hoyt 2007). We log–transformed red sea urchin density and then standardized log-transformed red sea urchin density by the overall maximum for statistical analyses.

We paired density measures from repeat sampling of the same transect where each pairing represents a count conducted pre-sea otter colonization (before) and post-colonization (after). The before and after periods are separated by 3 years, except the most recent period where the pre-impact period is represented by transects conducted over a 5 year period. Transects without repeat surveys and outside of red sea urchin habitat (e.g. soft sediment) were not used in our analyses. Transect counts made during the same period where sea otters did not occur during the

pre- and post-periods were used as controls. This approach allowed us to conduct analyses during four different time intervals based on the availability of sea otter occupation information (Table 1.1). In total four repeated measures two-way ANOVAs were performed to determine if the interaction between the period (before-after) and site (presence or absence of sea otters) was significant for sea otter recolonization occurring in 1997, 2000, 2003 or 2010 (Table 1.1, Smith 2006, Stewart-Oaten et al. 1986). Between 2005 and 2010, minimal survey effort was applied to red sea urchins by the ADF&G, as market conditions made for limited harvest within the study area by the commercial fleet; therefore, transects that were typically surveyed every 3 years were surveyed over a 5 year period (Hebert 2014) altering the pattern in our BACI design (Table 1.1). In all cases, only a single count was made in both pre- and post-surveys. We were unable to identify if red sea urchin density decreased significantly where sea otters had persisted for periods longer than three years, as ADF&G no longer conducts surveys when densities are reduced in the presence of sea otters. We did identify a single fishing area that was colonized by sea otters in 2003 and surveyed again in 2011. The ADF&G counted only 21 red sea urchins on 28 transects, with SCUBA divers noting that these red sea urchins were in crevasses (ADF&G, unpublished data, 2011). Further, ADF&G divers conducted surveys in 2011-2012 in areas known to be colonized by sea otters between 2010 and 2014 and recorded sea otter predation (presence of spines and broken urchin tests) on 25% of transects (ADF&G, unpublished data, 2014).

We examined the change in sea urchin density over time in fishing reserves (areas closed to commercial fishing) with and without sea otters. Spatially clustered transects were surveyed regularly by the ADF&G in two fishing reserves for red sea urchins (n=20 with sea otter

presence, n=20 without sea otters, Figure 1.2). Between 1997 and 2012, reserves with sea otters were surveyed 12 times and reserves without sea otters were surveyed 14 times. We calculated the mean density (i.e. urchins per m shoreline) and standard error for each reserve in each year a survey was completed and then conducted a weighted linear regression of densities on survey year, using the inverse of the variance as the weighting factor. We present the linear trends in red sea urchin density as a function of survey year and use an ANCOVA analysis to determine if the slopes of the linear relationships were significantly different between areas with sea otters present and absent.

Geoduck clams

We analyzed geoduck clam survey data collected by the ADF&G using SCUBA, with no more than twelve years lapsing between repeat surveys during 1997-2013. Divers counted geoduck "shows", defined as a divot or clam siphon consistent with that of a geoduck clam, along a 2 m wide predetermined transect. The survey method evolved from a linear shoreline density estimate, as was done for red sea urchins (# per m of shoreline), to an area estimate where transects were surveyed within a clam bed (# per m^2), both with their associated error, although diver counts along transects are comparable between methods (Pritchett and Hoyt 2007, Rumble and Siddon 2011). For the linear shoreline density estimate, total geoduck clams were counted along a transect conducted perpendicular to the shoreline from 0 - 18.3 m depth, and this count was divided by the total length of shoreline represented by the transect to obtain a linear density. A transect refers to a sampling event (i.e. count) at a particular location. We analyzed data from resampled transects, in which a repeat count was made at the same location, separated by at least two years during a pre- (1997-2006) and post- (2004-2013) period, hereafter called paired

transects (n=371 paired transects). Note that pre-and post-periods overlap as transect counts early in the pre-period could be paired with transect counts from early in the post-period. Paired transects were compared in impact and control sites. Impact sites occurred where sea otters were distributed as determined by a sea otter survey conducted in 2010 (n=211), and control sites occurred where the 2010 sea otter distribution did not overlap with geoduck clams beds (n=160, Figure 1.3). Due to limitations of the survey data, we were not able to account for differences in the time elapsed since recolonization, but we present the frequency distribution of the number of years between transect counts for the impact and control sites to assess whether differences in the time elapsed could affect results. All surveys were conducted in clam beds fished at a rate of 2% of the surveyed biomass annually. We log-transformed density data, as the densities were not normally distributed, and then standardized the transformed density of geoduck clams by the maximum observed transformed density across all transects (Smith 2006).

We assessed if our division of impact and control sites was representative of sea otter activity (large pits, broken geoduck clam shells) recorded by divers along each transect. We examined differences in geoduck clam densities during before and after periods at control and impact sites using both a paired *T*-test and a repeated measures two-way ANOVA with interactions BACI design (Smith 2006) (Table 1.2, Figure 1.3). Significance in the ANOVA interaction term suggests that geoduck clam density changes at different rates in the presence compared to the absence of sea otters (Stewart-Oaten et al. 1986). Due to the cryptic nature of geoduck clams and the potential for an individual clam to be misidentified or miscounted, as divers may be counting a divot or "show" instead of an actual clam, we removed outliers from the analyses. Outliers

were defined as transects with density measures beyond an upper limit, defined as 1.5 times the inter-quantile range corresponding to the 80th percentile.

Dungeness crab

We analyzed Dungeness crab catch data (pounds harvested, > 165 mm carapace width, males only) from 1969-2010 provided by ADF&G for fishing districts in central Southeast Alaska (ADF&G, unpublished data, 2014). Fishing years run from 15 June to 28 February with closures from 15 August to 1 October to protect female crabs during peak molting and mating (Stratman et al. 2014, Swiney et al. 2003). We refer to a fishing year by the year in which the fishing season begins, although the season extends into the following calendar year. Due to legal requirements of the state of Alaska, fisheries catch data is confidential if less than three permit holders harvest from a fishing district. Thirty-one fishing districts had sufficient non-confidential catch data for analyses, out of 44 total fishing districts in our study area (Figure 1.4, Table 1.3).

We modeled the catch of Dungeness crab as a function of fishing years in 31 fishing districts using both a linear regression model and a segmented (breakpoint) regression model with an unknown breakpoint to determine if sea otters were impacting Dungeness crab catch. Breakpoint models are commonly used in trend data when a known or unknown treatment exists and are particularly common in clinical studies (Wagner et al. 2002) but are used less frequently in an ecological context as the approach requires large amounts of pre-intervention data (Toms and Lesperance 2003). We hypothesized that if sea otters were having an impact on the catch within a fishing district, a breakpoint would be identified close to the year when sea otters first colonized the fishing district, and the slope of the second segment would be negative (decreasing

catches over time). Further, we modeled adjacent fishing districts not impacted by sea otters as controls. We hypothesized that control fishing districts would display different trends and would be less likely to show a breakpoint, i.e. the null (no trend) or a linear model would be a better fit to the catch data. For each fishing district, we used an analysis of variance (F-test) to determine which of the two models better represented the catch data, as the linear model is a reduced form of the breakpoint model. The parameters of the breakpoint model include the slope of the first segment and the intercept (as for the linear model), in addition to the breakpoint and a parameter representing the difference in the initial slope and the slope of the second segment. If this quasi-experimental approach were appropriately identifying sea otter impacts on commercial Dungeness catch, we hypothesized that the estimated breakpoints would occur later as the distance from the release site increased. To determine the relationship between estimated breakpoints and least cost distance from release site, we used a weighted linear regression using weights inversely proportional to the variance of the breakpoint estimates.

There was considerable variability in Dungeness crab catches within our study area in Alaska, similar to catches in other regions. For example, Dungeness crab catch varies temporally in California, Oregon and Washington as a function of large-scale transport variability in the early life history of the species (Shanks and Roegner 2007). Yet whether transport or some other factor causes variability in Alaska is not clear. Because a majority of fishing districts had one or multiple years of unusually large catches over our study period, we had concerns about the appropriateness of a linear regression approach in modeling catch, especially regarding the assumption of homogeneity of variance, which was frequently violated when regression diagnostics were examined. We attempted to transform catches to approximate normality using

Box-Cox transformations; however, transforming the catch data did not fully address the influence of large catch values. To identify if model diagnostics would improve without substantial changes to the modeled coefficients when large catch values were removed from the analyses, we subsequently remodeled all fishing districts with potential outliers removed. We identified potential outliers as catch values that exceed two times the interquartile range of the mean annual catches for a particular fishing district. We present the results of both the breakpoint model and reduced linear model for each fishing district with and without large catches removed. All analyses and mapping were completed using R version 3.0.2 (R Development Core Team 2010) and ARCGIS 10.1 (ESRI 2012).

Results

Red sea urchins

The density of red sea urchins decreased between the time period before and after sea otter colonization during all four periods investigated (1997, 2000, 2003, 2010), in the presence but not in the absence of sea otters, suggesting that sea otters, and not other factors, are responsible for decreases in sea urchin density (Table 1.1, Figure 1.5). Sea urchin density was higher in areas with sea otters compared to areas without sea otters during the pre-impact period only in the 2010 comparison (Table 1.1, Figure 1.5).

We found a significant difference in the density of red sea urchins between fishing reserves with and without sea otters and over time from 1997-2012 (*ANCOVA*, Factors: survey year, $F_{(1,21)} = 11.35$, $p = 0.003$; otter presence, $F_{(1,21)} = 204.94$, $p < 0.001$; survey year × otter presence $F_{(1,21)} =$

6.6, $p = 0.02$; Figure 1.6). Weighted linear regression implied differences in the trend of red sea urchin density over the surveyed period of reserves with and without sea otters; however, neither reserve showed the trend to be significant at the 0.05 level. Although fishing effort for red sea urchins was not distributed equally throughout our study area between 1994 and 2012, it was not likely impacting red sea urchin density at the spatial scale of our study area as areas in which fishing was present and sea otters were not present showed no differences in density over time (Figure 1.5).

Geoduck clams

SCUBA divers observed sea otter predation on 59% of all transects at impact sites and at 0 transects at control sites where sea otters have not colonized (Figure 1.3). The density of geoduck clams in southern Southeast Alaska decreased in the presence of but not in the absence of sea otters, as evidenced by the significant interaction term between site and period factors in the BACI analysis, suggesting that sea otters have impacted geoduck clams in the region (Table 1.2, Figure 1.7). The t-test confirmed this general result, as geoduck clam density on paired transects was significantly lower in the sea otter impacted sites between the before and after periods of the study (*paired T-test,* $t = 5.84$, $df = 168$, $p \leq 0.001$), while sites in which sea otters have not colonized did not show a difference in geoduck counts along SCUBA transects between time periods (*paired T-test,* $t = 0.96$, $df = 143$, $p = 0.339$). The number of years between surveys was distributed similarly between impact and control sites and ranged from 2 - 12 years for sites impacted by sea otters and 2-13 years for control sites (Figure 1.7 inset).

Dungeness crab

Dungeness crab catch in central Southeast Alaska between 1984 and 2010 decreased in the presence of sea otters. Results from our analyses identified breakpoint models as superior for all fishing districts in which sea otters and the Dungeness crab fishery overlapped (Tables 1.3-1.4). The estimated breakpoint (fishing year) for fishing districts that were recolonized by sea otters were strongly correlated with the known colonization timing of sea otters in our study area *(Pearson* $r = 0.83$, $p = 0.003$). In all fishing districts recolonized by sea otters, the second segment of the breakpoint model had a negative slope. Further, the estimated breakpoints occurred progressively later in areas that were further from the sea otter release (Figure 1.8), except fishing district 103-90, which is discussed below. The trend in the chronology of breakpoints as a function of least cost distance was particularly evident for fishing districts to the west of Kuiu Island, with a similar trend identified for the two fishing districts to the east of Kuiu Island but the impact seemed to be delayed as was sea otter colonization in these districts (Figures 1.4, 1.8). Weighted linear regression identified a significant relationship between least cost distance from release site and estimated breakpoints ($F_{(1,7)}$=6.46, p=0.039) implying sea otters have colonized Kuiu Island at 0.9 linear km y^{-1} (p=0.038; Figure 1.8). Fishing district 103-90, comprising Sea Otter Sound, had a small Dungeness crab fishery in isolated embayments in the extreme eastern side of the fishing district uncharacteristic of the region and was not included in the above regression analysis (Figure 1.4). Finally, the mean number of years between breakpoint estimates and the last observed catch (usually reported as confidential due to low participation) was 4.8 years (SE = 0.8).

Modeling results were different for fishing districts where sea otters colonized compared to fishing districts that were not colonized (Table 1.4). In uncolonized fishing districts, 62% of the time the null model (suggesting no trend in catch, i.e. catch remained stable over time) or the linear model were superior to the breakpoint model (Table 1.4). Further, 24% of fishing districts that did not overlap with sea otter presence exhibited a breakpoint model as superior with an estimated breakpoint during the 1991 or 1992 fishing year, followed by a negative slope (Tables 1.3-1.4). Only 14% of the fishing districts not colonized by sea otters exhibited a breakpoint outside the 1991/1992 period, with a negative secondary slope, as the superior model (Table 1.4).

When outliers were removed, linear and breakpoint models most often met regression assumptions, while results remained relatively consistent. When outliers were not excluded, the regression assumption of homogeneity of variance was not met in 74% of modeled fishing districts, which regression diagnostics suggested was due to extreme catches in certain years (Table 1.3). We identified at least one outlier in 77% of fishing districts (Table 1.3). Regression diagnostics improved when outliers were removed, with only 26% of subdistricts exhibiting noncompliance with regression assumptions, particularly homogeneity of variance (Table 1.3). Seventy-nine percent of fishing districts produced similar results with outlier removed or outliers present (i.e. superior model type was consistent, the estimated breakpoint was within 5 fishing years, and models estimated similar slopes, Table 1.3). All fishing districts in which sea otters and Dungeness crab catch overlapped had similar results (defined above) in breakpoint estimations with and without outliers included in the modeling procedure (Table 1.3).

Discussion

In Southeast Alaska, sea otters are associated with reduced abundance of geoduck clams, red sea urchins and Dungeness crabs. Our study and Larson et al. (2013) provide evidence that sea otters are threatening the commercial potential of nearshore commercial shellfish fisheries in the study area. The trend appears to persist as densities of red sea urchins and sea cucumbers and catch of Dungeness crab have not increased or rebounded after long-term sea otter colonization when a sea otter density declines.

Sea otters quickly reduce red sea urchin abundance and have great potential to reduce commercial fishing opportunity. Within three years sea otters significantly reduced sea urchins densities where they overlapped. We identified that extended presence (> 3 years) of sea otters reduced red sea urchins density to very low levels, but we could not demonstrate the extent of sea otter impacts beyond a three year period because the ADF&G does not survey areas with densities below a commercially-harvestable threshold. In a companion study conducted in rocky habitats recently colonized by sea otters, red sea urchins comprised > 95% of the sea otter diet, provided the highest biomass per unit of foraging effort, and were consumed at an average rate of 1.01 red sea urchins a minute (Chapter 3, Z. Hoyt, personal observation, 2011). Our results are not unique, as in Sitka Sound in northern Southeast Alaska, sea otters were the leading cause of a reduction of 25 million individual red sea urchins between December 1991 and February 1993 (Davidson et al. 1993). Fishing is having little impact on sea urchin density compared to sea otter predation, as evidenced by the result of no significant difference in the density between before-after periods for areas where fishing occurred and sea otters were absent. In addition, decline in

red sea urchin density was correlated with the presence of sea otters in fishing reserves, however where neither sea otter predation nor fishing occurred, sea urchin density remained similar. The low impact of fishing on sea urchin densities may be a result of low fishing effort due to the difficulty in marketing in this region (Hebert 2014).

Our findings suggest that sea otters were predating on geoduck clams, as early as 1997, within the study area, and that the density of geoduck clams decreased between 1997 and 2011 in the presence of sea otters. Geoduck clams are energetically costly for sea otters to acquire because of the effort needed to excavate up to 1 m below the seafloor. Kvitek et al. (1993) suggested that sea otters in Alaska had not yet learned to predate the deeply burrowing geoduck during a study conducted in 1989. Geoduck clams may have a depth refuge from sea otters, as geoduck clams occur to depths over 100 m and sea otters forage from the intertidal to 60 m with rare dives occurring to 100 m (Bodkin et al. 2004, Esslinger et al. 2014, Goodwin and Pease 1989, Newby 1975). Certain segments of the sea otter population (i.e. females with pups) do not predate on geoduck clams, likely because of the long dive times need to excavate a clam (Z. Hoyt, personal observations, 2011-2013). The ability for commercial densities of geoduck clams to persist in the presence of sea otter predation is supported by the fact that two commercial fishing districts exist where sea otters were first released at the Barrier Islands and Maurelle Islands in southern Southeast Alaska (sea otter persistence > 45 years). Geoducks are long lived and slow recruiting; therefore, the cumulative impact as identified in this study likely best describes sea otter impacts on geoduck clam fisheries. Further, soft bottom communities, that include geoduck clams have been described as being more resilient to sea otter predation, which may be a result of the cryptic

nature of organisms within subsurface habitat, the vastness of the habitat type, and recruitment characteristics of prey species within the habitat (Stewart 2011, Weitzman 2013).

Total catch of Dungeness crab declined in fishing districts where sea otters had colonized, while catches remained stable or increased in areas where sea otter were absent. Seven fishing districts impacted by sea otters and with an estimated breakpoint prior to 2004 and one with an estimated breakpoint in 2006 no longer support commercial Dungeness crab fishing. These results indicate that sea otter presence of approximately 5 years reduces Dungeness crab catch to a non-commercial level, which is slightly longer than the observed time in which sea otters reduced red sea urchin density to non-commercial levels (≤ 3 years). Three patterns in Dungeness crab catch were observed in fishing districts where sea otters were not present between 1969 and 2010: 1) no trend, 2) an increasing linear trend, and 3) a decreasing trend after an estimated breakpoint during the 1991 or 1992 fishing seasons, observed in five fishing districts in Frederick Sound. The estimation of a breakpoint in 1991/1992 is likely explained by a regulatory change in 1991 that implemented a moratorium on open access participation in the Southeast Alaska Dungeness crab fishery and granted future permits based on historical catch and participation (Stratman et al. 2014) This change caused higher fishing effort and inflated reporting immediately prior to its implementation in 1991.

Catch data provide an imperfect estimate of the abundance of Dungeness crab for multiple reasons. First, catches only reflect legal males, as females or sub-legal males are not harvested. Sea otters, on the other hand, are not selecting by sex but likely are selecting on size of crab. Dungeness crabs were present in the diet of sea otters in newly colonized and long established

areas, but in the long-established areas, the crabs were smaller than is commercially harvestable (Z. Hoyt, personal observations, 2011-2013). Second, the catch is a function of fishing effort, which has contracted spatially as sea otters have reduced fishing area (i.e. more pots fished in a smaller area), and is determined by economic factors, such as fluctuations in the price of Dungeness crab and fuel (J. Stratman, personal communication, 2015), making it challenging to untangle the impacts of sea otters on Dungeness crab stocks in Southeast Alaska.

Dungeness crab catch is typically variable where it is commercially exploited, limiting the ability to model linear trends in the data (Higgins et al. 1997). Results where models with and without outliers deviated (6%) and where regression assumptions did not hold (26%) after the removal of outliers should be interpreted with caution. However, 74% of the time, our approach meets assumptions, and 80% of the time the results were the same with and without outliers. If the impacts were subtle, a non-linear approach could be appropriate, but our simple approach appears to be sufficient.

Although little is known of the ecosystem state of southern Southeast Alaska prior to the fur trade (pre-1800), Russian fur records translated in 2014 indicate that in a ten year period, between 1801 and 1811, approximately 46,000 sea otters were harvested in Southeast Alaska suggesting the carrying capacity of the region may be at least double the population estimated in 2011 (Katrina Wessls, USFWS, personal communication, 2014, USFWS 2014). About 41% of the potential sea otter habitat (area < 60 m in depth) in Southeast Alaska has not been colonized, and large red sea urchin barrens and Dungeness crab stocks are still available as both prey and

commercial resources (Hebert 2014, Stratman et al. 2014, Chapter 3). Therefore we expect sea otters to continue to limit the biomass of commercial shellfish in Southeast Alaska under current management. Finally, it is important to note that although the commercial potential of shellfish fisheries may be limited in Southeast Alaska due to the recolonization by sea otters, the ecological sustainability of these invertebrate species is not in jeopardy, as sea otters and these prey have coexisted since the Pleistocene (Riedman and Estes 1990).

Accurately determining the biomass consumed of commercial shellfish by sea otters would provide important information for resource managers and industry. In certain marine mammal predator-prey interactions the prey removal can approach or exceed that from a commercial fishery (Bax 1991, Larson et al. 2013, Laws 1977, Markussen et al. 1992, Ray et al. 2006, Rice et al. 2011). However, the ability to accurately quantify spatially and temporally varying parameters (i.e. age and sex specific sea otter energy budgets, abundance estimates, size and prey specific predation rates) associated with such estimates is complex and we encourage future research in this area. During the 2013-14 reporting period, 2.34×10^6 kg of shellfish (geoduck clams, red sea urchins, sea cumbers and Dungeness crab) were harvested from Southeast Alaska (Hebert 2014, Stratman et al. 2014) while sea otters arguably consumed 2.62×10^7 kg of commercial shellfish annually, based on a 2012 estimate of 25,712 sea otters (USFWS 2014), consuming 20% of their bodyweight daily (Costa and Kooyman 1982), a mean sea otter weight of 30.4 kg (n = 19, Z. Hoyt, personal observation, 2011) and 46% of the population level diet consisting of four shellfish (Chapter 3). Although our estimate of annual shellfish consumption by sea otters should be refined, it provides support that not only are sea otters responsible for

declines in shellfisheries but an order of magnitude difference between predator and fisheries removal exists.

Future sustainability of shellfish fisheries in Southeast Alaska is questionable in the presence of this growing sea otter population. Fisheries management of shellfish when sea otters are present could be improved with information on natural mortality from predation, and represents an important step forward towards an ecosystem-based approach to fisheries. Trends in predator abundance could be used to explicitly model predation mortality, as was done for walleye pollock for three predators including Stellar sea lions (Hollowed et al. 2000), and in theory could improve stock assessment models. Our results indicate that the reduction in abundance of commercial shellfish varies by species and is a function of both sea otter pressure and shellfish life history. Therefore, information is needed at the species level to inform fisheries management. The challenge in the current management system is that sea otters are managed under a conservation framework, and shellfish fisheries are managed under a sustainable yield framework that is parameterized without natural mortality from this top predator. Management goals for the predator and prey contradict one another. The ability for both frameworks to adapt to one another will likely be outpaced by the recolonization of sea otters in the study area. As noted by Beverton (1985) the world into which marine mammal populations are recovering is different from that before large industrial exploitation occurred. Indirect competition between marine mammals and fisheries resources is expected to increase globally (Trites et al. 1997). Indirect positive benefits from sea otters to nearshore fish species including black rockfish (*Sebastes melanops*), a commercially important species in California, have been documented as a result of piscivory, linked to increased giant kelp abundance (Markel and Shurin in press).

Positive indirect interactions should be a research priority as the future of shellfisheries is likely limited by the increasing distribution of sea otters across the north Pacific. Additionally, future research to link marine mammals to fisheries and scientifically based and adaptable management frameworks are needed to manage complex marine mammal and fisheries interactions.

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Tables

Table 1.1 Red sea urchin (a) Before-after, control-impact (BACI) design and (b) results from repeated measures two-way ANOVA analysis comparing standardized red sea urchin density (urchins per m shoreline) between sites (presence or absence of sea otters), period (before/after impact), and their interaction for sea otter impacts occurring in 1997, 2000, 2003 and 2010.

(a) Summary of red urchin paired transects used for BACI ANOVA design. [a]

Sea otter colonization	"Before" years	"After" years	Paired transects ($n/2$)	
			Otters present	Otters absent
1997	1994-1996	1997-1999	47	192
2000	1997-1999	2000-2002	39	216
2003	2000-2002	2003-2005	28	235
2010	2005-2009	2010-2012	56	106

(b) Red urchin density among periods, sites (impact) and their interaction. [b]

Year of sea otter impact	Source of variation	df	MS	F	p
1997	Period	1	7.80	2.793	0.095
	Site	1	28.12	10.059	0.002**
	Period x Site	1	19.60	5.528	0.008**
	Residuals	472	2.80		
2000	Period	1	0.89	0.364	0.547
	Site	1	29.54	12.072	<0.001**
	Period x Site	1	40.88	16.705	<0.001**
	Residuals	506	1240.6	2.454	
2003	Period	1	3.30	1.338	0.248
	Site	1	60.53	24.512	<0.001**
	Period x Site	1	80.71	32.685	<0.001**

Table 1.1 continued

	Residuals	524	2.796		
2010	Period	1	87.62	42.41	<0.001**
	Site	1	86.14	41.70	<0.001**
	Period x Site	1	125.39	60.70	<0.001**
	Residuals	320	2.07		

[a] Period compares before and after while impact compares sites with and without sea otters. Sample size ($n/2$) represent the number of paired red sea urchin transects used in the analysis during each time period.

[b] Analyses were performed in areas with confirmed sea otter presence between the before and after period for impact sites and areas confirmed with no sea otter presence for corresponding 6 year periods for control sites. Data reported include p values, F statistics, degrees of freedom (df), and mean squares (MS). Critical p values were adjusted using the Bonferroni correction; significance levels are indicated as follows: ***, $p < 0.001$, and **, $p < 0.01$.

Table 1.2 Geoduck clam (a) Before-after, control-impact (BACI) design and (b) results from repeated measures two-way ANOVA analysis comparing standardized geoduck clam density among sites (presence or absence of sea otters), period (before/after impact), and their interaction.

(a) Summary of geoduck clam paired transect used for BACI ANOVA design. [a]

Sea otter impact	"Before" years	"After" years	*n/2*
Present	1997-2005	2006-2013	173
Not Present	1997-2006	2004-2013	144

(b) Geoduck clam density among periods, sites (impacts) and their interaction. [b]

Source of variation	df	MS	*F*	*p*
Period	1	0.20653	9.874	0.002**
Site	1	0.00142	0.068	0.795
Period x Site	1	0.06143	5.528	0.017*
Residuals	622	0.02733		

[a] Period compares before and after while impact compares sites with and without sea otters. Sample size (*n*) represent the number of paired geoduck clam transects used in the analysis.
[b] Analyses were performed in areas with confirmed sea otter presence between the before and after period. Data reported include *p* values, *F* statistics, degrees of freedom (df), and mean squares (MS). Significance levels are indicated as follows: **, $p < 0.01$, and *, $p < 0.05$ *.

Table 1.3 Results from regression analyses conducted individually on the annual catch of Dungeness crab fishing districts between 1969 and 2010 in central Southeast Alaska impacted or adjacent to fishing districts impacted by sea otters. Included are model results for fishing districts with outliers identified (2.0 times the interquartile range of the raw catch data), included and removed to demonstrate that results are robust to violations of regression assumptions (homogeneity of variance).

Fishing district	Year of known sea otter coloniz-ation)[a]	Slope of linear model[b]		Breakpoint estimate (*SE*)		Change in break-point	Slope of breakpoint model segments		Best fit model[b]	
		Outliers included	Outliers removed	Outliers included	Outliers removed		Outliers included	Outliers removed	Outliers included	Outliers removed
110-16	N	(+) ***	(+) ***	1999 (3.3)			(+)(-)		BP *	
110-32[c,d]	N	(+)	(+)	1978 (2.5)	1978 (2.7)	0.2	(+)(-)	(+)(-)	BP *	BP **
108-60	N	(+) ***	(+) ***	2008 (1.3)			(+)(-)		LM	
110-33[c]	N	(+) *	(+)	1977 (2.7)			(+)(-)		LM	null
110-14[c]	N	(+) ***	(+) ***	1975 (3.1)	1975 (3.5)	0.4	(-)(+)	(-)(+)	LM	LM
108-30[c]	N	(+) **	(+) ***	1982 (4.6)	1983 (7.5)	-1.5	(+)(+)	(+)(+)	LM	LM
110-12[c,d]	N	(+) ***	(+) ***	1985 (5.4)	1973 (1.9)	11.9	(-)(+)	(-)(+)	LM	BP *
109-43[c]	N	(+) ***	(+) ***	1986 (7.1)	1986 (4.7)	-0.5	(+)(-)	(+)(+)	LM	LM
110-34[c,d]	N	(+)	(+) **	1992 (5.1)	2007 (2.8)	-15.1	(+)(-)	(+)(-)	null	LM
106-30	N	(+) ***	(+) ***	1994 (10.8)			(+)(+)		LM	
106-43[c,d]	N	(+) ***	(+) ***	2002 (3.6)	1985 (5.1)	17.1	(+)(-)	(+)(+)	LM	LM
105-32[c,d]	N	(+) ***	(+) ***	2002 (3.7)	1996 (3.1)	6.2	(+)(-)	(+)(-)	LM	BP **
110-23[c]	N	(+) ***	(+) ***	2003 (8.9)	2005 (8.4)	-1.9	(+)(+)	(+)(+)	LM	LM
106-44	N	(+) ***	(+) ***	2007 (1.6)			(+)(+)		LM	
110-22[c]	N	(+) ***	(+) ***	2008 (2.7)	1999 (8.3)	8.2	(+)(-)	(+)(+)	LM	LM
106-42[c,d]	N	(+) ***	(+) ***	2004 (1.9)	2005 (1.7)	-0.6	(+)(-)	(+)(-)	BP *	null
110-24[c,d]	N	(+)	(+)	1991 (4.3)	1992 (5.3)	-0.7	(+)(-)	(+)(-)	BP *	null
110-31[c,d]	N	(+)	(+)	1991 (2.4)	1992 (2.5)	-1.0	(+)(-)	(+)(-)	BP ***	BP ***
110-13[c]	N	(+) *	(+) **	1991 (2.9)	1992 (3.2)	-1.0	(+)(-)	(+)(-)	BP ***	BP **
108-50[c]	N	(+)	(+)	1991 (4.4)	1989 (4.1)	2.4	(+)(-)	(+)(-)	BP *	BP *
110-15	N	(+) *	(+) **	1992 (3.0)	1993 (3.0)	-1.0	(+)(-)	(+)(-)	BP **	BP **
109-62[c]	1994	(-)	(-)	1984 (2.8)	1985 (2.4)	-1.1	(+)(-)	(+)(-)	BP **	BP ***
109-51[c]	2003	(-)	(-)	1987 (2.7)	1992 (2.8)	-5.3	(+)(-)	(+)(-)	BP ***	BP ***
109-52[c]	1997	(+)	(+)	1995 (3.5)	1994 (3.4)	1.1	(+)(-)	(+)(-)	BP **	BP **
105-31[c]	1997	(+)	(+)	1997 (2.9)	2001 (1.5)	-3.9	(+)(-)	(+)(-)	BP **	BP ***
109-45[c]	2003	(+)	(+) *	2000 (2.0)	2001 (1.6)	-1.0	(+)(-)	(+)(-)	BP ***	BP ***
106-41[c]	2010	(+) **	(+) **	2004 (1.3)			(+)(-)		BP ***	
109-30[c]	2010	(+) ***	(+) ***	2004 (2.4)			(+)(-)		BP *	

Table 1.3 continued

109-44	2010	(+) ***	(+) ***	2006 (1.1)	2006 (0.8)	0.0	(+)(-)	(+)(-)	BP **	BP **
103-90[c]	2010	(+) ***	(+) ***	2007 (0.8)	2006 (1.2)	1.0	(+)(-)	(+)(-)	BP **	BP **
109-42	2010	(+) ***	(+) ***	2008 (0.8)	2008 (1.5)	-0.3	(+)(-)	(+)(-)	BP *	BP *
	Combined Standard Error			91.3	94.4					

[a] N denotes areas not colonized by sea otters prior to 2010

[b] Significance levels of slope and ANOVA results of the full model BP (breakpoint) and reduced model LM (linear) as follows: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. The null model is the case where a linear models slope did not differ from 0.

[c] Fishing districts where residuals did not imply homogeneity of variance with outliers present.

[d] Fishing districts where residuals did not imply homogeneity of variance with outliers removed.

Table 1.4 Percentages of superior models describing Dungeness crab catch as a function of fishing year in 31 fishing districts. Four categories where identified defining model results in fishing districts colonized and not colonized by sea otter in central Southeast Alaska.

	Breakpoint		Linear model (represented by a + slope)	Null model (No significant trend predicted)
	≠ 1991 or 1992	= 1991 or 1992		
Sea otters present (n=10 fishing districts)	100%	0%	0%	0%
Sea otters absent (n=21 fishing districts)	14%	24%	57%	5%

Figures

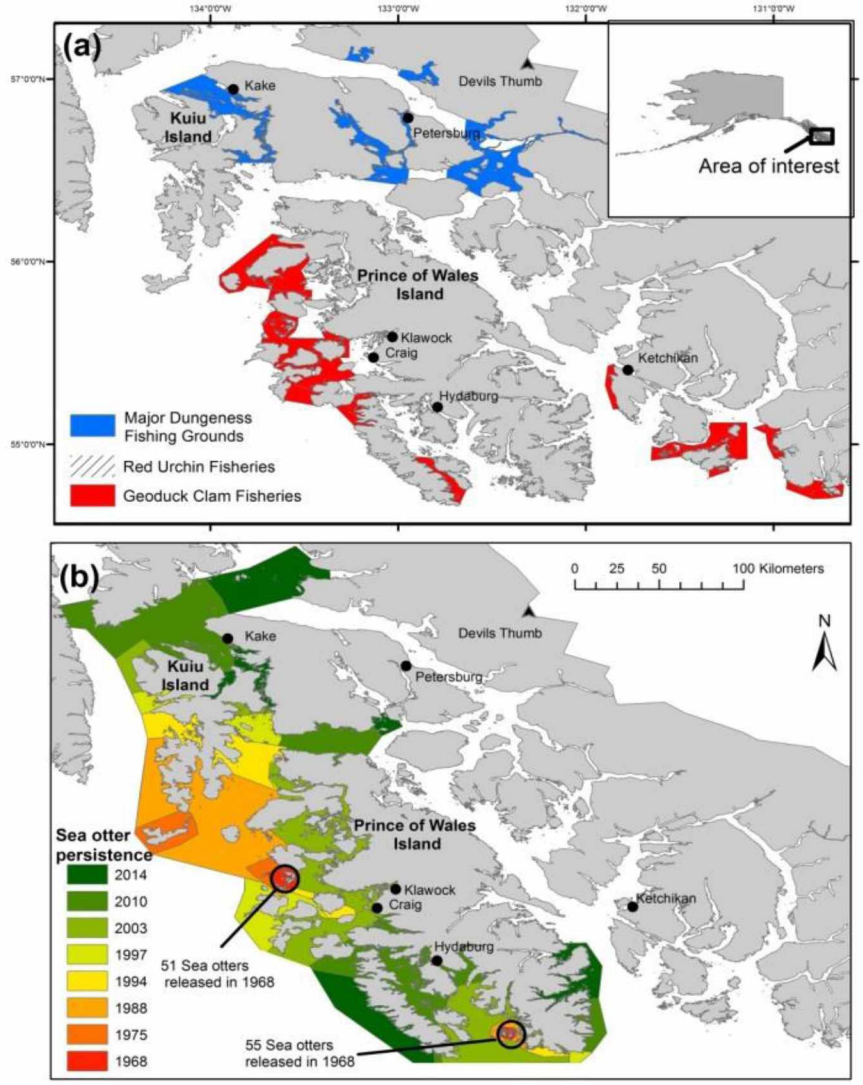

Figure 1.1 The study area in southern Southeast Alaska including the distribution of commercial shellfisheries and sea otters. (a) The 2014 distribution of three commercial shellfisheries including Dungeness crab, red sea urchin and geoduck clams. The Dungeness crab fishery is open throughout Southeast Alaska and this map only depicts the productive fishing grounds defined by the Alaska Department of Fish and Game. The red sea urchin and geoduck clam fisheries are restricted to the area depicted in panel (a) within the study area. (b) The distribution of sea otters determined by census and survey efforts conducted since the release of 106 sea otters to the region in 1968 at two release sites (depicted as circles, Burris and McKnight 1973, Esslinger and Bodkin 2009, Hodges et al. 2008, Johnson et al. 1983, Pitcher 1989, Schneider 1975, USFWS 2014).

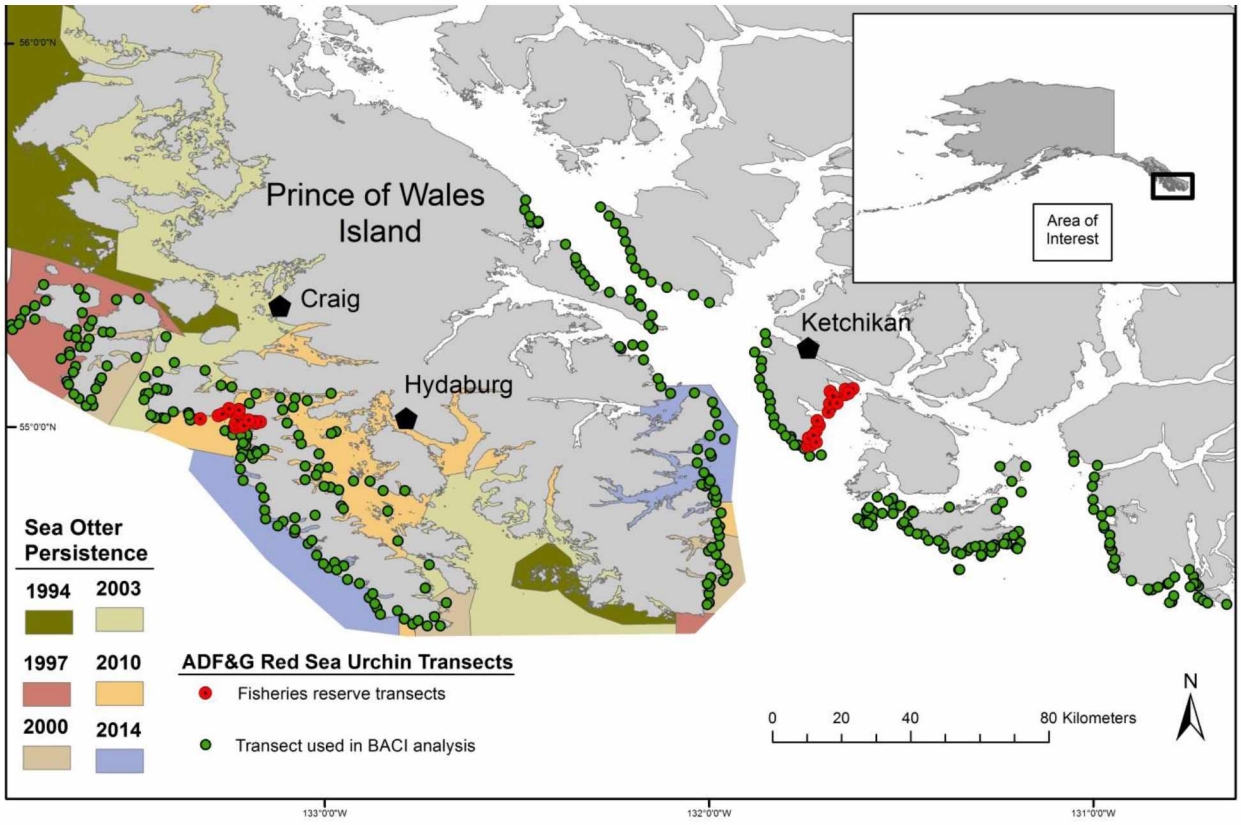

Figure 1.2 Red sea urchin transects and sea otter persistence, determined by distribution surveys and local and traditional knowledge interviews, used in before-after, control-impact (BACI) analyses in southern Southeast Alaska. Transects completed in fisheries reserves are highlighted (Esslinger and Bodkin 2009, Hodges et al. 2008, USFWS 2014, A. Rice, Alaska Marine Advisory Program, personal communication 2014).

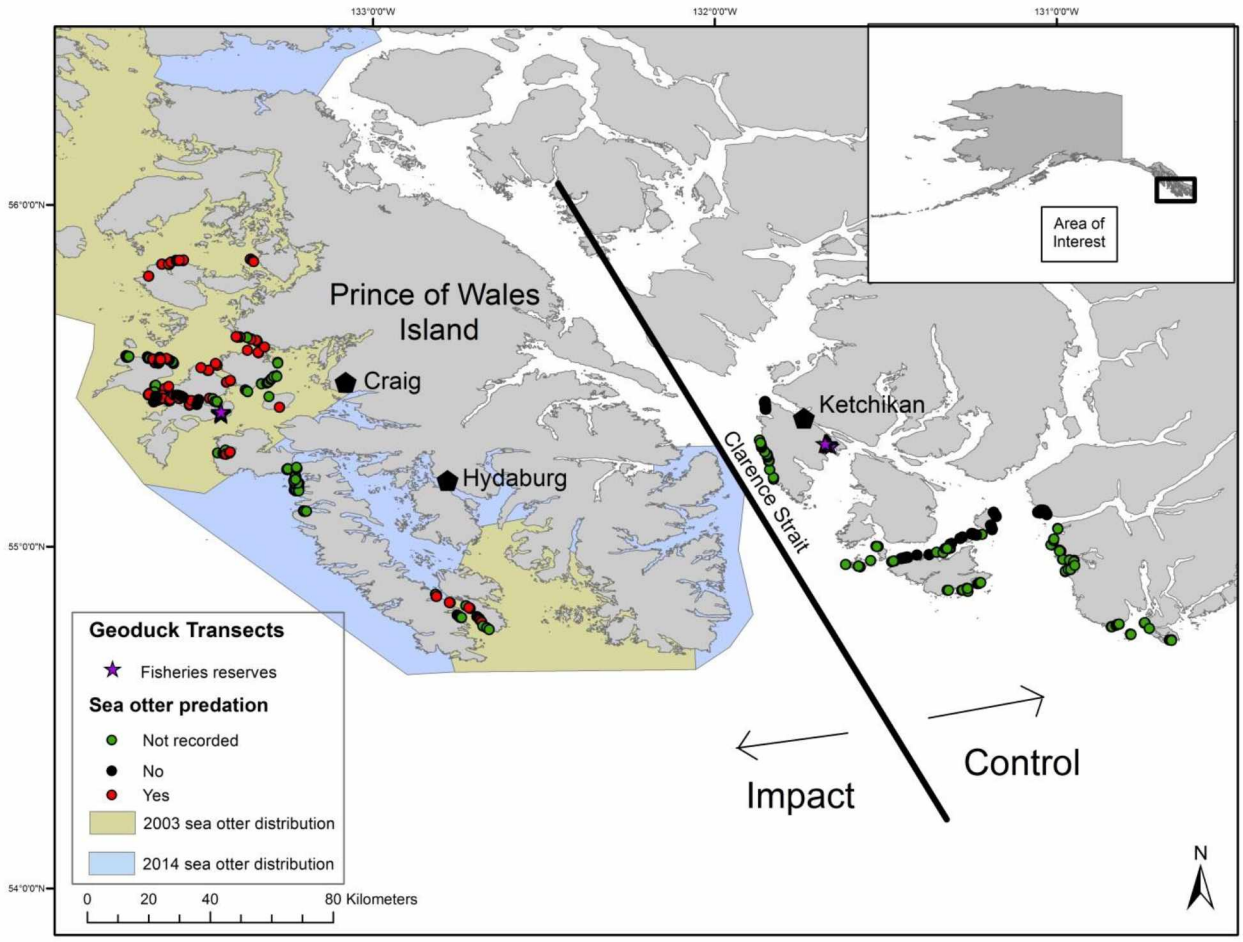

Figure 1.3 Geoduck clam transects and sea otter distribution, representing area which has been colonized by sea otter and area which sea otters have not colonized used in the before-after, control-impact analysis in southern Southeast Alaska. Transect are depicted as having the presence of sea otter predation recorded by SCUBA divers while counting geoduck clams (ADF&G, unpublished data, 2014). Additionally, transects within two no fishing reserves are shown. The distribution of sea otters from aerial surveys conducted in 2003 and 2014 are shown (USFWS 2014, Chapter 3).

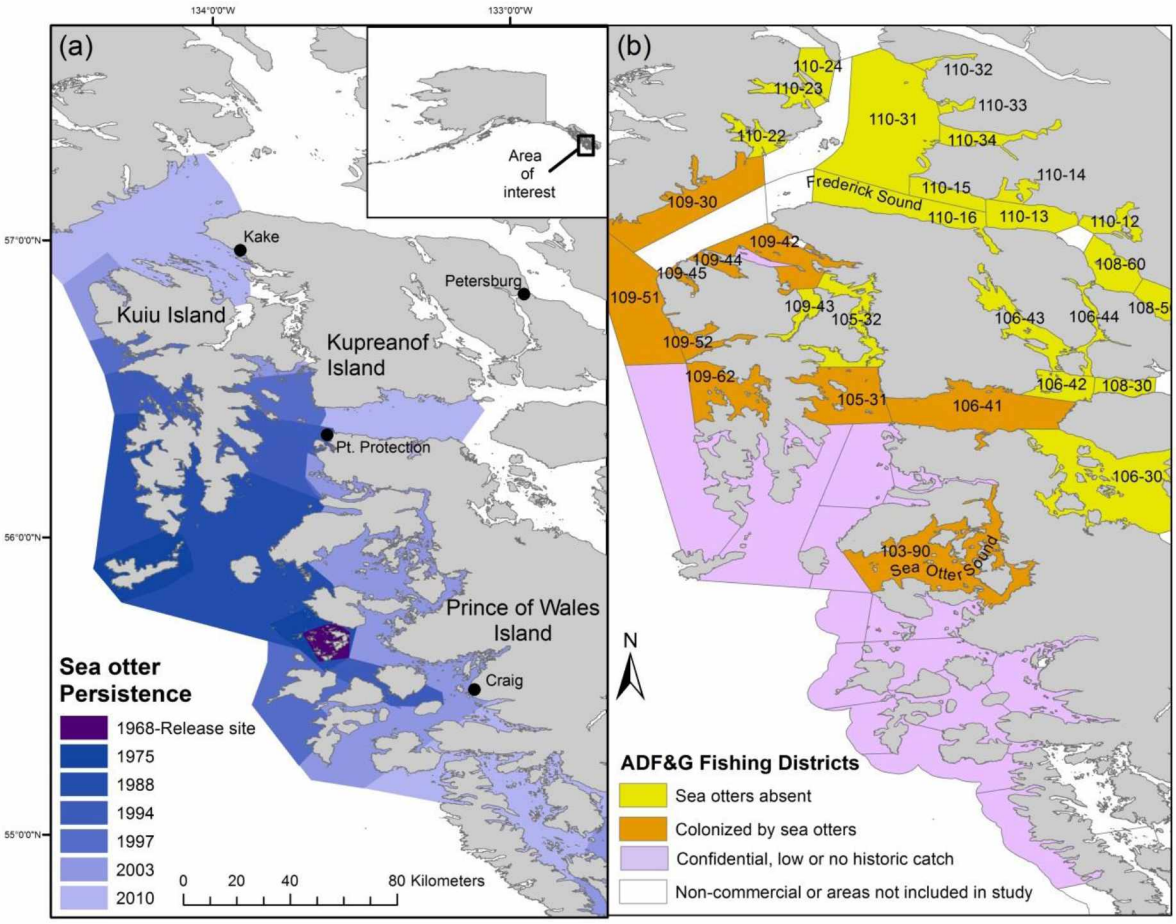

Figure 1.4 a) Sea otter persistence and b) Dungeness crab fishing districts from which commercial catch data was used for analyses of sea otter impacts on Dungeness crab catch. Labeled fishing districts were used in the analyses.

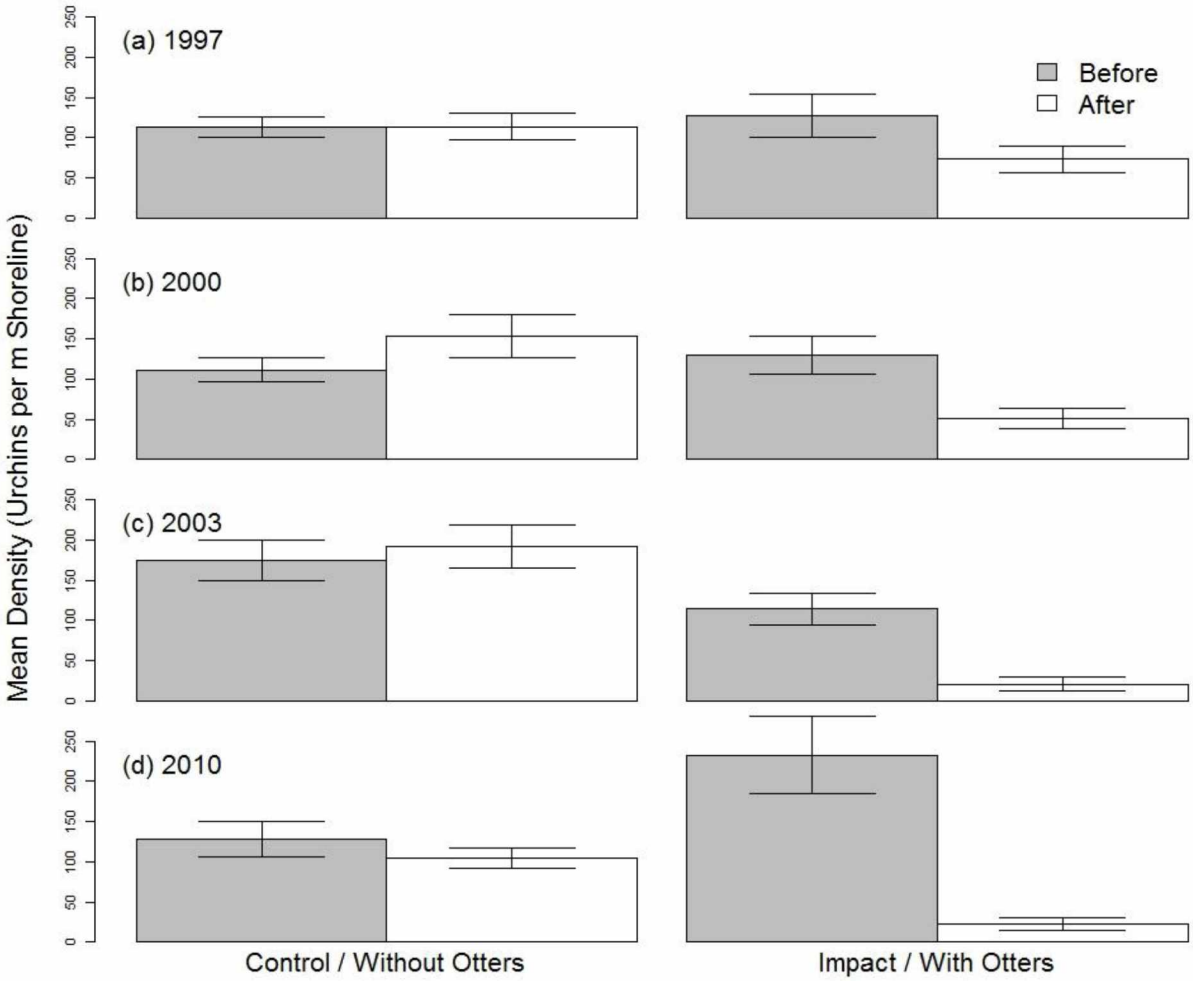

Figure 1.5 Mean red sea urchin density before and after the presence of sea otters and control transects without sea otters during individual impact periods, error bars represent 95% confidence intervals. Comparisons were done separately for paired transects with known sea otter occupation in 1997 (a), 2000 (b), 2003 (c), 2010 (d).

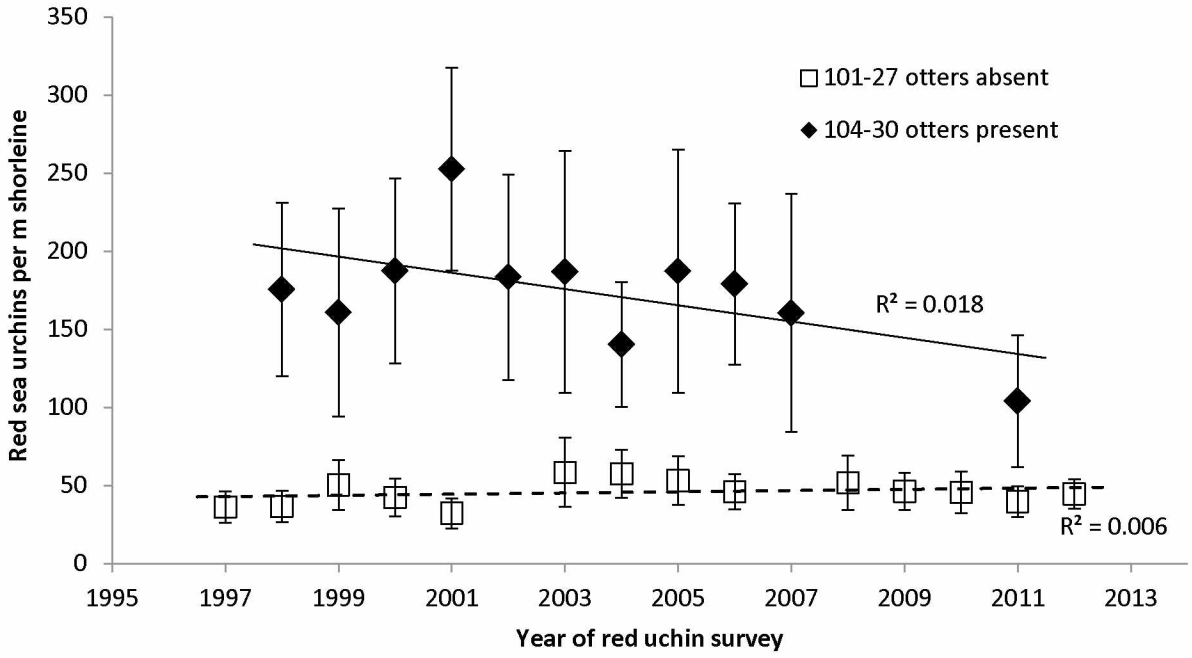

Figure 1.6 Time series of the mean red sea urchin density calculated from transect completed in two fishing reserves. Reserve 101-27 (n = 20 transects) is located in an area in which sea otter have not colonized, whereas reserve 104-30 (n = 20 transects) was colonized by sea otters between 2003 and 2010. Trend lines are presented but do not imply a significant trend (101-27, $F(1,12) = 0.73$, $p = 0.778$ and 104-30, $F(1,9) = 1.98$, $p = 0.192$). Error bars represent 95% confidence intervals for individual surveys. A significant difference between the slopes of the linear trends was identified (ANCOVA, $F(1,21) = 6.6$, $p = 0.018$).

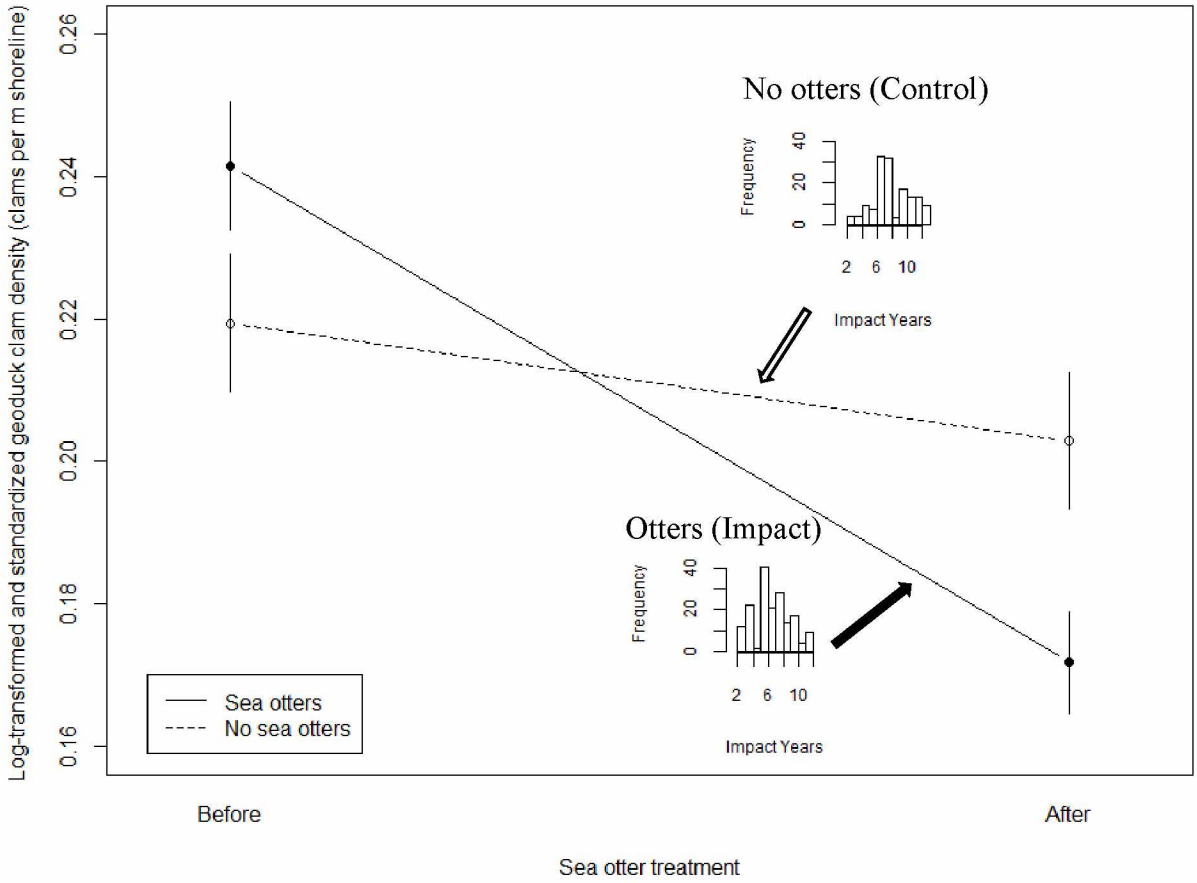

Figure 1.7 Interaction plot of a sea otter treatment on geoduck clam density in southern Southeast Alaska. The response variable is the log-transformed standardized mean shoreline density of geoduck clam transects. The treatment is the presence or absence of sea otters. Error bars represent ± 1 SE. The embedded histograms depict the frequency distribution of the number of years between surveys of paired transects for impact and control areas.

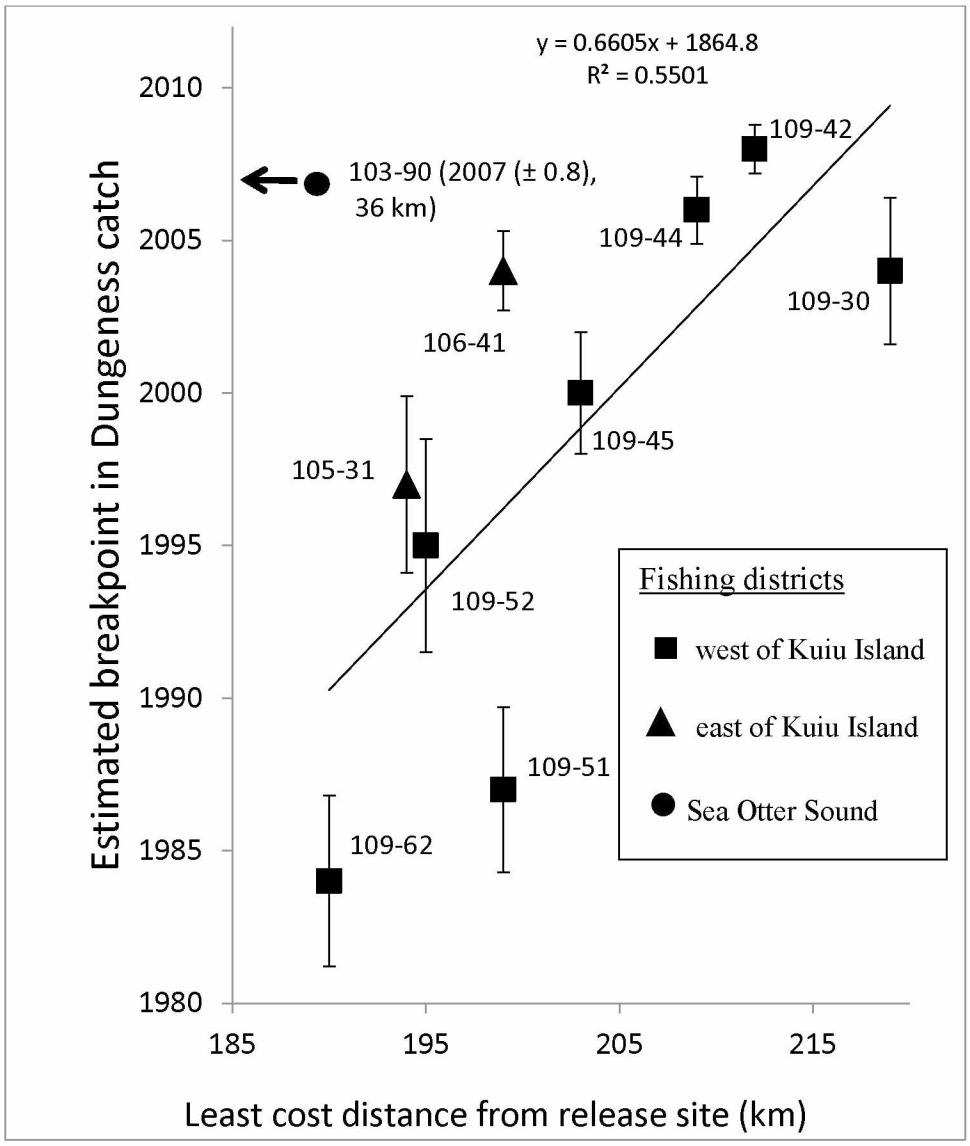

Figure 1.8 Relationship between estimated breakpoints and least cost distance from centroid of ten Dungeness crab fishing districts and sea otter release site in central Southeast Alaska. The location of fishing districts, mapped in Figure 4, related to Kuiu Island is designated by the legend. Error bars represent the standard error of the estimated breakpoint. A weighted linear regression identified the relationship was significant ($F(1,7) = 6.46$, $p = 0.039$) implying sea otters have colonized Kuiu Island at 0.9 linear km y-1 ($p = 0.038$) Note: Fishing district 103-90, comprising Sea Otter Sound, had a small Dungeness crab fishery in isolated embayments in the extreme eastern side of the fishing district uncharacteristic to the region and was not included in the regression analysis.

Chapter 2: Space use of northern sea otters (*Enhydra lutris kenyoni*) within an exploited and growing population[2]

Abstract

Conservation and management of carnivore populations, whether the goal is to increase the distribution through translocation efforts or to reduce the distribution to avoid human conflicts, can include insights from spatially explicit modeling at the landscape level. To that goal, we studied changes in space use over time in Southeast Alaska where sea otters are in conflict with fisheries and are exploited by coastal Alaska Natives. We monitored movements of 30 sea otters implanted with VHF transmitters from May 2011-April 2014 near Kake, Alaska, a location at the distributional edge of this expanding population. We collected a total of 1056 geolocations from these animals using aerial and ground-based telemetry. We then evaluated habitat selection and generated models of occurrence based on a bivariate normal probability distribution function and the following covariates: (1) hunting pressure, (2) exposure, (3) canopy kelp coverage, (4) bathymetry, (5) distance to shore, and (6) terrestrial habitat. Models were fit separately for each individual and results grouped by females, territorial males and non-territorial males. Because sea otter harvest increased around Kake during the study, we compared space use before (2011-2012) and after (2012-2014) this increase in hunting. Non-territorial males and females segregate; non-territorial males primarily used protected bays, whereas females used habitats with canopy kelps. Covariates influencing territorial males were more variable and showed overlap in selection parameter estimates with both female and non-territorial males. Modeled

[2] Hoyt, Z.N., G. L. Eckert, M.T. Tinker, V.A. Gill. Prepared for submission in Ecological Applications.

space use between pre- and post-hunting time periods was reduced by 24%, suggesting reduction in the area occupied by this population in response to hunting. The reduction in space use was largely observed for females and non-territorial males, as space use remained relatively unchanged for territorial males throughout the study. The distribution of the growing sea otter population in Southeast Alaska is most influenced by hunting pressure and habitat segregation between non-territorial males and females.

Keywords

Resource selection, VHF telemetry, synoptic model, marine mammal, subsistence hunting

Introduction

The management of carnivore populations, whether to conserve a threatened species or to control the abundance of one, requires a basic understanding of the relationship between the available resources and use of those resources by the species (Ripple et al. 2014). The overlap between human populations and predators typically results in competition for prey resources and habitat and is at the heart of most conflict between carnivores and humans (Treves and Karanth 2003). Livestock depredation by carnivores and the reactionary killing of predators by humans is an example of competition for space and a worldwide conservation concern (Mishra 1997, Treves et al. 2004). The conflict arises because human financial interests are compromised, as are conservation goals. Sea otters are another example of a species whose prey resources overlap with humans, causing direct conflict (Carswell et al. 2015, Garshelis and Garshelis 1984, Larson et al. 2013, Riedman and Estes 1990). Management of conflicts are typically top-down strategies, including eradication, regulated harvest, and preservation of the predator, all of which require an understanding of a population's use of space and resources (Treves and Karanth 2003). Regulated harvest, or hunting is typically concentrated in areas that are accessible to humans or where the environment and economics make it feasible (Novaro et al. 2000). Thus, hunting has consequences on the spatial distribution of human prey at the landscape level. Here we examined how a growing predator population is distributed at the landscape level as a function of environmental variables, intraspecific competition, and hunting pressure.

Most marine top predators are known to be sensitive to variability in their environment, notably through changes in their distribution (Forney 2000). Therefore, creating models that correctly

describe a predator's space use and preferred habitats is critical to conservation and management strategies. Space use of an apex predator is often dictated by the distribution of its prey and intraspecific competition; however, when the predator is not an apex predator or impacted by human disturbance, space use may be additionally influenced by interspecific variables (Spitz et al. 2012). For instance, hunting may impact space use directly by the removal of predators or indirectly by disrupting the distribution or age structure of a population, both of which may release lower trophic levels from predation (Milner et al. 2007, Terborgh et al. 2010). If lower trophic levels are a food source for humans, the understanding of habitat use by the predator becomes critical to manage conflicts between predator and resource exploitation.

Sea otters in Southeast Alaska have experienced multiple conservation challenges, including extinction, reintroduction, exponential growth, conflict with humans for resources and increased hunting pressure all within the last century (Burris and McKnight 1973, Estes 1990, Kenyon 1969, Larson et al. 2013). To elaborate, sea otters were exploited by Russian, British and American fur traders from 1741 until protected internationally in 1911 (Kenyon 1969). According to a recent examination and translation of archival documents from the Russian American Company, by the mid to late 1830s sea otters were functionally extinct from Southeast Alaska, as a result of the fur trade (K. Wessels, personal communication). Beginning in 1965, sea otters were reintroduced at six locations along the outside coast of Southeast Alaska (Burris and McKnight 1973). The remote nature of these relocation sites, the low density of humans and ample prey resources were likely factors that facilitated population growth of sea otters in the region. Thus, by the late 1990's, the sea otter population had grown significantly (increasing 8-13% annually since 1990) and began colonizing inside protected waters of Southeast Alaska

prior to 2003 (Esslinger and Bodkin 2009, USFWS 2014). Numerous surveys conducted regionally throughout Southeast Alaska from 2005-2012 estimated the sea otter abundance in Southeast Alaska at approximately 25,000 individuals (USFWS 2014). The absence of sea otters from Southeast Alaska for over a century facilitated the development of subsistence and commercial shellfisheries, including pinto abalone (*Haliotis kamtschatkana)* and Dungeness crab (*Metacarcinus magister),* and the subsequent recolonization of sea otters has led to resource conflicts between this predator and humans (Woodby et al. 2005). These fisheries conflicts could be one factor in the increased harvest of sea otters by coastal Alaska Natives, who are legally allowed to harvest sea otters for subsistence purposes in Alaska, and reported harvest increased from an average of 322 individuals annually prior to 2010 to 1,497 individuals in 2013 across Southeast Alaska (USFWS 2014). The sea otter population will likely continue to experience conservation challenges well into the next century in Southeast Alaska as it continues to grow and recolonize more habitat.

Sea otter space use has been investigated by others, including studies on home range of individuals (Breed et al. in review, Jameson 1989, Lafferty and Tinker 2014, Laidre et al. 2009, Loughlin 1980) and range expansion of the California population (Lubina and Levin 1988, Tinker et al. 2008). In California and Washington most sea otters, particularly females, exhibit high site fidelity and occupy relatively small home ranges (4-104 ha), sometimes consisting of more than one distinct centers of use; however, some males move more extensively over greater distances (Breed et al. in review, Jameson 1989, Lafferty and Tinker 2014, Laidre et al. 2009, Ralls et al. 1996, Riedman and Estes 1990). Further, sea otter populations tend to be spatially segregated according to demographic and reproductive status (Garshelis et al. 1984, Kenyon

1969, Loughlin 1980): specifically, (1) females with and without pups form groups, near easily accessible prey and typically away from the range edge; (2) territorial males defend territories from other males in areas that females frequent for mating purposes; and (3) less dominant, typically younger (or very old) males form bachelor groups, often near the range peripheries (Garshelis and Garshelis 1984, Garshelis et al. 1984). Our study complements these previous studies in that it documents space use of an expanding and exploited sea otter population.

We examined space use of sea otters by addressing three questions within our study site in Southeast Alaska. (1) Sexual segregation: Do different segments of the population use different areas or habitats? (2) Hunting: Has hunting pressure affected sea otter space use or distribution within our study site? (3) Range expansion: Can we identify a change in landscape level space use over three years of study? To address these questions we chose to focus on a segment of the Southeast Alaska population (hereafter referred to as a population) of sea otters near Kake, Alaska, and near the edge of the expanding geographic range in May 2011 (USFWS 2014). This population experienced an increase in hunting related mortality beginning in October 2012, as assessed from reported subsistence hunting to the U.S. Fish and Wildlife Service. The results of our study are timely for the management and conservation of sea otter populations across the North Pacific Ocean.

Methods

Thirty sea otters (n = 16 males, 14 females) were captured and implanted with VHF transmitters (Advanced Telemetry Systems, Isanti, MN) between 17-26 May, 2011, near Kake (Figure 2.1), using established protocols (Monson et al. 2001, Ralls et al. 1989). During the handling and

surgical procedures a pre-molar tooth was extracted for aging (Matson's Laboratories, Milltown, MT). Ages ranged from 1 to 7 years for females and 1 to 8 years for males, and we made the assumption that we captured a representative sample of the local sea otter population (Appendix Table 2.A-1). Sea otters were released at or near the capture location and no mortalities or behavioral changes were observed as a result of capture.

Sea otters were relocated using VHF telemetry techniques outlined by Amlaner and Macdonald (1980) from fixed wing aircraft, small vessels and stationary data loggers from 29 May, 2011 – 1 April, 2014. The mean time between locations for all individuals over the course of our study was 22 days. To address the inherent autocorrelation in our telemetry fixes, we filtered our data by removing records that were collected near in time and space to one another by randomly selecting one location per individual for each 22 day interval of the study period.

We used a multivariate or synoptic model for describing animal space use that estimates an individual's probability of occurrence as a function of the individual's association with a fixed spatial area, environmental covariates and hunting density. Synoptic modeling of animal space use was introduced by Horne et al. (2008) and follows the general framework developed by Manly et al. (2002) and refined by Johnson et al. (2008). The structure of the modeling procedure compares a null model of space use to a series of models with one or more covariates. This technique allows for a clear interpretation of each covariate by estimating a selection parameter (β).

The null model we used for our analysis was the bivariate normal probability density function:

$$f_0(x,y) = \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}}\ exp\left[\left[-\frac{1}{2(1-\rho^2)}\right]\left[\left[\frac{x-\mu_{xy}}{\sigma_{x1}}\right] - \left[\frac{2\rho[x-\mu_x][y-\mu_x]}{\sigma_x\sigma_y}\right] + \left[\frac{y-\mu_y}{\sigma_y}\right]^2\right]\right], \quad (2.1)$$

where ρ is the correlation coefficient of the x and y coordinates, σ_x and σ_y are the standard deviations and μ_x and μ_y are the means of the x and y values, respectively. Sea otters have a tendency to bias their movements toward a central place, such as a kelp bed, social rafting area or foraging ground (Jameson 1989, Laidre et al. 2009, Loughlin 1980). A bivariate normal probability density function has been used to characterize the space use of species who exhibit site fidelity (Horne et al. 2008, Okubo and Levin. 2001).

The modeling structure assumes a proportional increase or decrease in $f_0(x)$ as a result of including spatially defined covariates. Covariates were assigned to each location used in our analysis and included (1) terrestrial boundary or land, (2) bathymetry (water depth), (3) degree of exposure to prevailing winds and waves, (4) proportional coverage by canopy-forming kelps, (5) the relative frequency of occurrence of subsistence sea otter takes (hunting), and (6) distance from shore. Details of the data sources and computational methods for each of these variables are provided in Table 2.A-2. We included both a linear and quadratic term for the bathymetry covariate in our modeling procedure, as sea otters forage at intermediate depths less than 100 m (Bodkin et al. 2004). All covariates were standardized between 0 and 1 before model parameters were estimated to provide more efficient computing and to standardize selection surfaces. We assessed collinearity of our covariates before modeling space use, which can inflate selection coefficients and error terms (Menard 2002), and found all pairwise correlations to be less than ρ = 0.687.

We divided the landscape of the study site into 5.76 x 10^4 m^2 grid cells (240 m x 240 m). We selected this resolution because 240 m was the observed mean error in locating radio tagged sea otters during our study. Each grid cell was then assigned a defined value for each covariate (using standard GIS-based tools).

The synoptic model takes the form:

$$\boldsymbol{s(r)} = \frac{\boldsymbol{f_0(r)} \prod_{i=1}^{k} \boldsymbol{(1 + \beta_i H_i(r))}}{\sum_{j=1}^{m} \left[\boldsymbol{f_0(r_j)} \prod_{i=1}^{k} \boldsymbol{\left(1 + \beta_i H_i(r_j)\right)} \right]}, \tag{2.2}$$

where *s(r)* is the probability of an animal being located in grid cell *r*, *m* is the number of grid cells in the landscape, $H(r)$ is the value of each environmental covariate at grid cell *r*, ranging from 0 to 1 (in the case of categorical variables, $H(r)$ = 1 if the covariate is equal to a given level and 0 if not), β is an estimated selection parameter controlling the magnitude of the effect of the covariates, and *k* is the number of covariates used in the model. The denominator in equation 2.2 scales probabilities *s(r)* to sum to 1 over the entire study site. We did not estimate the selection parameter (β) for the terrestrial boundary covariate but rather fixed it at -1 such that s(r) = 0 on land as sea otters rarely use terrestrial space. All other parameters including the five spatial parameters and the selection parameters for each covariate where estimated by maximizing the log likelihood function:

$$L(\boldsymbol{\theta}, \boldsymbol{\beta}) = \sum_{q=1}^{n} ln\left[\frac{f_0(r_q|\boldsymbol{\theta}) \prod_{i=1}^{k}\left(1 + \boldsymbol{\beta}_i H_i(x r_q)\right)}{\sum_{j=1}^{m}\left[f_0\left((r_j|\boldsymbol{\theta})\right) \prod_{i=1}^{k}\left(1 + \boldsymbol{\beta}_i H_i(r_j)\right)\right]}\right], \quad (2.3)$$

where θ is a 5-dimensional vector of parameters describing the probability density function for the null model of space use $f_0(r)$, and β is a k-dimensional vector of parameters selecting for or against covariates.

Sixteen ecologically plausible, *a priori* competing models were constructed to describe the space use for individual non-territorial male, territorial male and female sea otters over the entire timeframe of the study and during the pre- (May 2011-September 2012) and post- (October 2012 –May 2014) hunting periods. We used a small-sample corrected Akaike information criterion (AICc) to rank the sixteen *a priori* models within each model set (Johnson and Omland 2004). Within each model set we calculated Akaike weights for each model i (w_i), which are values representing the relative weights of evidence that model i is the best model within the set. When there was not a single model with $w_i \geq 0.95$, we considered competing models with cumulative weights ≥ 0.95. For each model set, a model-averaged selection coefficients ($\hat{\beta}$) was estimated as the weighted average across competing models in which that particular variable was included using their relative w_i as weights (Manly et al. (2002). Model-averaged estimates of the covariate selection parameters ($\hat{\beta}$) were used to assess the relative influence of different covariates on the probability of finding a sea otter in a grid cell. For any positive value of the covariate function ($H(x) > 0$), when $\hat{\beta}$ is < 0, there is a proportional decrease in the utilization distribution, when $\hat{\beta} = 0$ there is no change, and when $\hat{\beta} > 0$ there is a proportional increase in the utilization distribution, which allowed us to evaluate covariates individually. Further, we calculated

confidence intervals as outlined by Manly et al. (2002) for each model set using variance estimates obtained from a Hessian matrix which was computed as part of the optimization procedure (Nocedal and Wright. 2006) to determine if a significant avoidance or selection (i.e. confidence intervals do not bound zero) existed for each individual throughout the study and for pre- and post- hunting intervals. All computations and analyses were conducted in R version 3.0.2 (R Development Core Team 2010).

Sexual segregation

Through field observations we identified 3 functional groups of sea otters within our study site, described as territorial males, non-territorial males and females (both with and without pups). To identify if our field observations were supported by space use models, we examined the model-averaged selection parameters ($\hat{\beta}$) estimated from competing models and their associated confidence intervals for each radio-tagged sea otter for the model set representing the entire study period (pre-and post-hunting) to determine if differences in space use existed between the three functional groups. Further, to visualize potential differences in space use between these functional groupings, we then mapped an average probability density surface for each functional group across the landscape expressed as the cumulative probabilities of occurrence for each grid cell *r* for each functional group.

Hunting

In addition to the hunting density covariate, which examines the spatial overlap of hunting with sea otters, we also compared change in space use during two time periods. We segregated our telemetry data into pre- (May 2011-September 2012) and post- (October 2012 –May 2014)

hunting periods for each individual. To reduce the bias of uneven sample size in our study design, we only used individuals in this analysis that were monitored for the duration of the study (n = 17). We then compared the selection coefficients of the model covariates for each individual in both pre- and post-hunting periods to identify if differences were present.

Range expansion

We determined the average probability of occurrence in each grid cell *r* across the landscape from each individual during both pre- and post-hunting periods. We then computed cumulative space use polygons for both periods by selecting all grid cells (*r*) representing < 90% (general use area) and < 75% (core use area) of the cumulative probability distribution summed across individuals, and mapped the probability density surface and associated polygons to determine if significant space use occurred outside of the limits of the 2011 population distribution.

Results

We obtained 1056 geo-locations from 30 individual sea otters. Data from 8 individual sea otters were not used in the analysis for various reasons including natural or unknown mortality (n = 3), transmitter failure (n = 2) and unknown signal loss (n = 3). Further, an additional 5 individual sea otters had insufficient data for the pre-/post-hunting analysis, as we were unable to monitor them throughout the study due to subsistence hunting mortality (n = 1), natural morality (n = 1) and signal loss (n = 3). Three individuals were harvested by subsistence hunters late in the study but still allowing sufficient data to model the space use in both the pre- and post-hunting periods. After filtering the telemetry data and removing individuals with insufficient data for modeling purposes, we had an average of 35 (SD 7.4) usable locations per individual (n = 22).

Tagged animals that we relocated did not appear to disperse widely from their original capture site. However, non-territorial males did make large movements (> 40 km) but always returned to areas near their capture in the core study area. Females and territorial males showed a high degree of site fidelity. Finally, all population segments of sea otter selected for intermediate depth (Figure 2.2) with no discernable differences between population segment or pre-/post-hunting period.

Sexual segregation

Females

All of the competing models for individual females (n = 8) included a positive selection coefficient ($\hat{\beta} > 0$) for the kelp covariate (Figure 2.3, Table 2.A-1). The exposure covariate was positively selected ($\hat{\beta} > 0$) in 75% of the candidate models (Figure 2.3, Table 2.A-1). Within our study site, exposed areas with canopy kelps are typically headlands, reefs and islands adjacent to Frederick Sound (Figure 2.4). The estimated selection parameters ($\hat{\beta}$) for the distance from shore, bathymetry and hunting density covariates were present in the majority of best fit models for females; however, the precise nature of these effects differed between individuals. Thus, while these variables were clearly important to female habitat use, the details were not consistent. In general, the strong selection for canopy kelps (which occur at 5-20 m depth) in addition to a combination of effects from depth and distance to shore resulted in female habitat use that was largely restricted to the nearshore between the intertidal zone and 20 m depth contour (Figure 2.4).

Non-territorial males

In contrast to females, non-territorial males (n = 10) selected for protected areas ($exposure\ \hat{\beta} < 0$), as the exposure covariate was present in 60% of the candidate models (Figure 2.3, Table 2.A-1). The kelp covariate was present in all but one (90%) of the candidate models for non-territorial males; however, unlike females, non-territorial males exhibited a negative selection for canopy kelps (Figure 2.3, Table 2.A-1). Non-territorial males, like females, demonstrated no consistent pattern in the selection for or against the bathymetry, distance to shore and hunting density covariates, and the null model of space use was the lowest ranking model in all non-territorial males. The bathymetry covariate, which included both a linear and quadratic term, suggested non-territorial males, not unlike females, selected for intermediate depth as the linear term was typically positive and the quadratic term negative, and individual differences were observed (Figure 2.3). Although model averaged selection parameters did not differ markedly between females and non-territorial males for the bathymetry or distance to shore covariates, non-territorial males appeared to select deeper areas (Figure 2.4). Within our study site, nearshore areas with little exposure, void of canopy kelps having moderate depth are best described as embayments (Figure 2.4). On multiple occasions we observed rafts of > 400 individuals of non-territorial males in sheltered embayments and on a single occasion observed a raft > 600 individuals.

Territorial males

The territorial males (n = 4) monitored throughout the study showed a high degree of individuality in the presence and value of covariates in candidate models, which precludes

conclusions for the group as a whole as done for females and non-territorial males (Table 2.A-1). The null model was the lowest ranking model in all but one of the territorial males, in which case it was the second lowest ranking model and all covariates were present in at least one candidate model for territorial males (Table 2.A-1). Territorial males demonstrated the highest degree of site fidelity, compared to females and non-territorial males. Two territorial males were never recorded outside of their known territory, a third was observed on three occasions outside of its known territory during winter, and the fourth spent approximately two months outside of its known territory annually in late winter. Three of the four territories bordered one another within the study site, and the fourth was adjacent to a non-territorial male area. The core or 75% cumulative probability of space use was used to measure the territory size of the four territorial males, and the average size of a territory was 4.38 km^2 (SD 1.88).

Hunting

Subsistence hunting was the leading source of mortality of radio-tagged individuals during the three-year study period with 4 instrumented individuals (n = 2 female, n = 2 non-territorial males) reported taken by Alaskan Natives. (Note: an additional non-territorial male was found on the beach, likely killed by hunters and unreported.) During 2013, following the increase in harvest, field crews observed that sea otters became intolerant of boats and aircraft.

Territorial males appeared to be uninfluenced by hunting during the study, as they remained closely or entirely associated with their territory. Territorial males showed little difference in the presence or value of selection parameters ($\hat{\beta}$) within candidate models representing pre- and

post-hunting periods and were similar to values estimated for the entire study period (Figures 2.3, 2.5, Table 2.A-3).

The hunting covariate was present in 88% of candidate models for both females and non-territorial males during the pre-hunt period of the study and when present was positive, except for one individual (SSE20) (Figure 2.5). In contrast, during the post-hunt period this covariate was negative and present in 57% of the candidate models for female and non-territorial males, with the same exception (SSE20) (Figure 2.5, Table 2.A-3). The two non-territorial males harvested in the post-hunting period of the study (SSE30 and SSE31), in addition to the individual we suspect was harvested (SSE03), did not select for or against hunting pressure (candidate models did not include the hunting covariate).

We determined positive selection ($\widehat{\beta} > 0$) for canopy kelp by females during both pre-and post-hunting periods (Figure 2.5). Although kelp was present in the majority of non-territorial male candidate models in both pre-and post-hunting periods, the selection parameter estimates and associated confidence intervals bounded zero suggesting non-territorial males did not strongly select for or against the canopy kelp covariate (Figure 2.5).

Range expansion

Space use of sea otters expanded between May 2011 and September 2012 and then contracted when hunting pressure increased (Figure 2.6). The mean 90% probability of space use from all sea otters monitored throughout the study (n = 17) during the pre-hunt portion of the study indicated that distribution of space use extended beyond the range edge determined by a 2011

population survey of the area and measured 341 km^2 (Figure 2.6). During the second half of our study, October 2012-May 2014, the population had contracted its space use in the general use areas (90% space use isopleth) to 264 km^2 and was similar in distribution to that observed in the 2011 population survey. Space use appeared to be retracted from areas near Kake where hunting density was highest (Figure 2.6). The core area of space use (75% space use isopleth) decreased from 66 km^2 during the pre-hunt period to 39 km^2 during the post hunt period. These results indicate that sea otters had moved away from hunting pressure and were using a more concentrated distribution of space during the post-hunt portion of the study.

Discussion

Our analyses revealed a number of interesting and previously unreported aspects of sea otter space use. First, the area used by sea otters expanded during the initial phase of our study (as one might expect in an expanding population) but subsequently contracted as hunting pressure increased. Areas of highest hunting density overlapped with the areas of range expansion, and sea otters subsequently avoided these areas. Secondly, different sea otter population segments exhibited different habitat preferences, with the result that female and non-territorial male sea otters were segregated spatially from one another throughout our study, supporting intraspecific competition for space use. Spatial segregation of the sexes is evident across the range of the species (Garshelis et al. 1984, Laidre et al. 2009, Loughlin 1980, Schneider 1978) but the consequences of sexual segregation in structuring a population are not well understood. In Prince William Sound, Alaska during studies conducted in the early 1970's and early 1980's, non-territorial male areas were located in both exposed habitats and embayments near the edge of the range and females avoided exposed areas (Garshelis et al. 1984, Schneider 1978). We found that

non-territorial males used protected embayments, while females used more exposed areas with abundant canopy kelps. Unique to our study, females with pups were found on the very edges of the population range.

Territorial males held the same territories throughout the study, with one territorial male leaving his territory for several months in late winter and then returning. In Alaska and California it has been reported that territorial males defended territories in areas of high female density, but often abandoned their territories for part of the year (Garshelis et al. 1984, Jameson 1989, Lafferty and Tinker 2014). Differences in the annual fidelity of territorial behavior between previous studies and ours are likely explained by a constant availability of receptive females within our study site and adequate prey availability within the territories due to only recent sea otter occupation. We observed newly born pups during all months of the study and could not discern any seasonality in pupping, as has been observed in other studies (Jameson 1989, Riedman and Estes 1990). The lack of seasonality in pupping within our study population is likely a result of high quality protected habitat and prey resources, therefore physiological instead of environmental factors are likely dictating pup timing. Boyd (1991) concluded that weather and nutrition are likely factors in the seasonal nature of reproduction within sea otter populations.

The protected nature and high availability of prey at our study site, which was colonized by sea otters between 2006-07, determined by local and traditional knowledge surveys (A. Rice, personal communication, 2014), drives the sexual segregation and site fidelity we observed. Space use did not appear to differ seasonally, which may be a result of the protected nature of our study site. To avoid any seasonal bias in our space use analysis we attempted to relocate sea

otters during all months, with 59% of the usable geo-locations collected between 1 July and 1 January and 41% collected between 2 January and 30 June over the three years of sampling. Females selected habitats where protection and caloric needs were most efficiently acquired (canopy kelp beds) and dominant males defend territories in these areas for reproductive purposes. Therefore, less dominant, non-territorial males were apparently excluded from canopy kelp beds, providing evidence for intraspecific competition and similar to the results described by Lafferty and Tinker (2014) in California. Within our study site, non-territorial males were associated with soft bottom habitats in protected embayments.

At the onset of the study we anticipated that instrumented sea otters would colonize new unexploited habitat as the population density increased due to intrinsic growth and immigration, and after prey resources were reduced. Although we did observe such movements into new areas for the first 18 months of the study, during the following period space use contracted and was likely limited by hunting. The lack of range expansion is likely due to animals being removed from the population (reduced density) and avoidance of hunting pressure.

Subsistence hunting was the leading cause of mortality in our study, with a minimum of 13% of the tagged individuals being taken, with no one segment of the population targeted. Bodkin and Ballachey (2010) concluded that sea otter populations could sustain hunting pressure but variables including sex ratio, reproductive and growth rates were crucial to set harvest goals. Although sea otters have a history of being effectively depleted in the North Pacific, the impact of hunting on population dynamics is largely unexplored. Gorbic and Bodkin (2001) noted that over the 18^{th} and 19^{th} century only about 1.5% y^{-1} of the global sea otter population were

harvested; however, this led to range-wide reduction and extirpation as harvest was not allocated to the density and distribution of the species. According to historic records from the Russian American Company the harvest rate was substantially higher in Southeast Alaska with 45,882 reported sea otters harvested between 1800 and 1809 followed by a decline in the reported harvest until the mid to late 1830s, with only a few harvested annually thereafter (K. Wessels, personal communication). The unexpected increase in subsistence hunting pressure and resulting change in space use during our study provided evidence that both inter- and intra-specific variables impact sea otter distribution.

During the initial pre-hunt portion of our study, space use extended beyond the 2011-surveyed distribution, and intraspecific competition was driving habitat selection. Prior to 2011 the southern Southeast Alaska sea otter population was increasing its distribution by approximately 117 $km^2 y^{-1}$ and increased in abundance at a rate of 12% annually (Hoyt et al. 2014). However, the substantial increases in hunting starting in October 2012 led to a contraction in space use of the population away from newly colonized areas and hunting pressure, likely adding substantial interspecific competition to the sea otter population structure. However, we were unable to model pre- and post-hunt periods for each population segment as further division of telemetry data would limit model fitting performance. Further, sea otters became intolerant of human presence, consistent with many exploited populations (Millspaugh et al. 2000). The modeled reduction in space use was likely a consequence of non-territorial males contracting their use of space from areas with the highest hunting densities, as hunting density was highest in protected areas without canopy kelps (areas non-territorial males selected for over the entire course of the study), which coincided with the closest habitat type and population segment to the community

of Kake. Although modeled sea otters' space use retracted and became more concentrated during the post-hunting portion of the study, three study animals were taken by hunters near the edge of the reduced distribution. These sea otters were unable to avoid hunting, likely due to the sedentary nature of sea otters and relatively small home-range and territory size of the species which lends itself to serial depletion (Garshelis and Garshelis 1984, Jameson 1989). We conclude that harvest strategies should consider spatial scale and sexual segregation, whether they are designed to reduce the number of sea otters or conserve a population. In addition, analysis of spatial, temporal, and demographic patterns of contemporary sea otter harvest in Southeast Alaska is needed to elucidate which segment of the population is receiving the most pressure and how that may impact population dynamics based on our findings.

Our model of space use provides useful insight to conflicts between sea otter and humans; however, additional information on habitat, spatially explicit prey abundances or predation could inform a more explicit model. Further, sea otter populations occur at various densities and distributions throughout the Pacific Rim and display divergent trends over relatively small spatial scales; therefore, modeling space use for different populations is necessary (Bodkin and Ballachey 2010, Riedman and Estes 1990). Further, model validation could improve the predictive abilities of the model procedure which could inform conflicts regarding range expansion, translocation sites or harvest strategies for sea otter or other sedentary species. The enhanced knowledge of space use will be advantageous to understanding future conflicts between predators and humans such as fisheries, oil and gas development or subsistence hunting.

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Figures

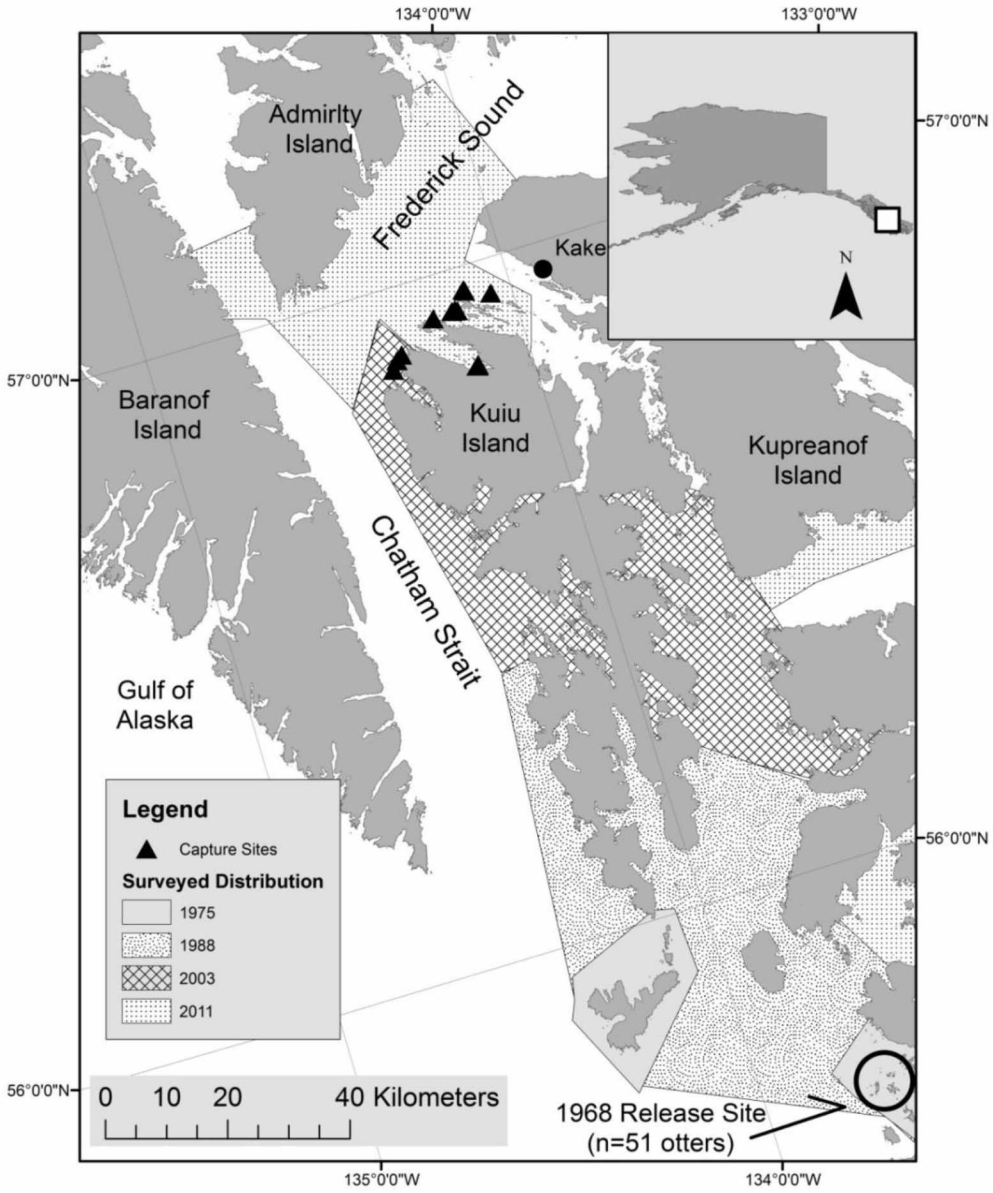

Figure 2.1 The study site near the coastal community of Kake in Southeast Alaska. The capture locations of 30 sea otters are symbolized as well as the translocation sites, and distribution of sea otters reported from surveys spanning 1975-2011.

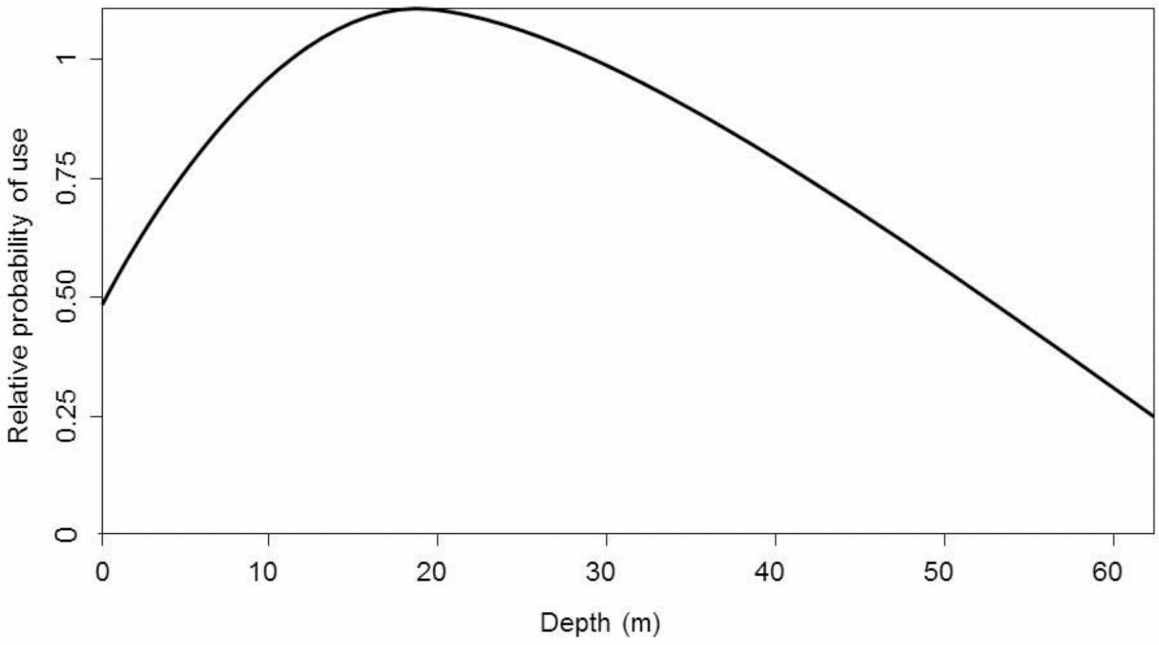

Figure 2.2 Predicted quadratic relationship between the relative probability of use and bathymetry (m) based on the modeled space use by sea otters The highest probability of space use occurred at 20 m and was similar for all population segments.

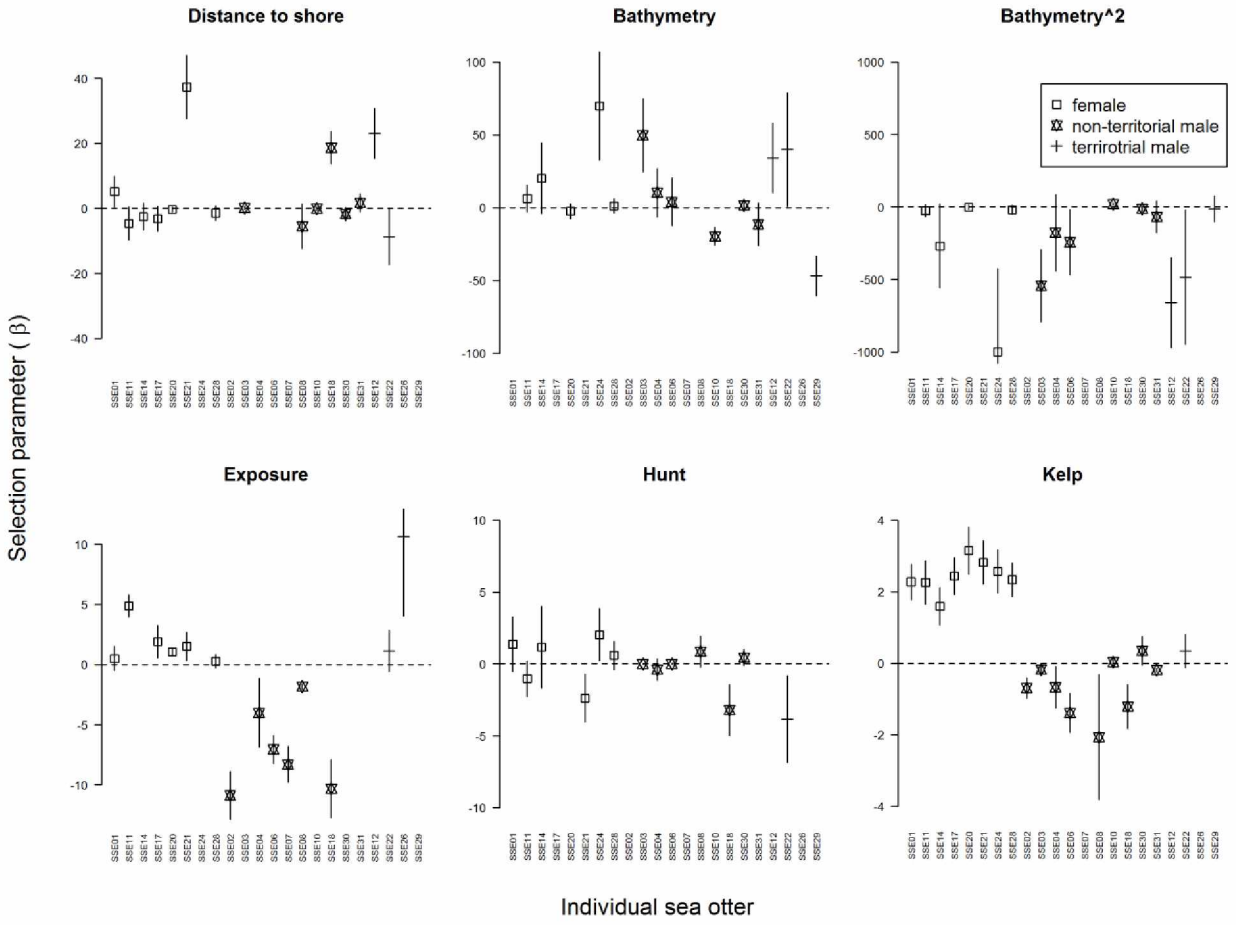

Figure 2.3 Standardized selection coefficients for females, non-territorial males and territorial males for six covariates used to model space use. Points represent the model average of coefficient estimates, error bars represent 1 SD. The y-axis in each plot is the scale of the standardized selection coefficient and the x-axis represent individual sea otters.

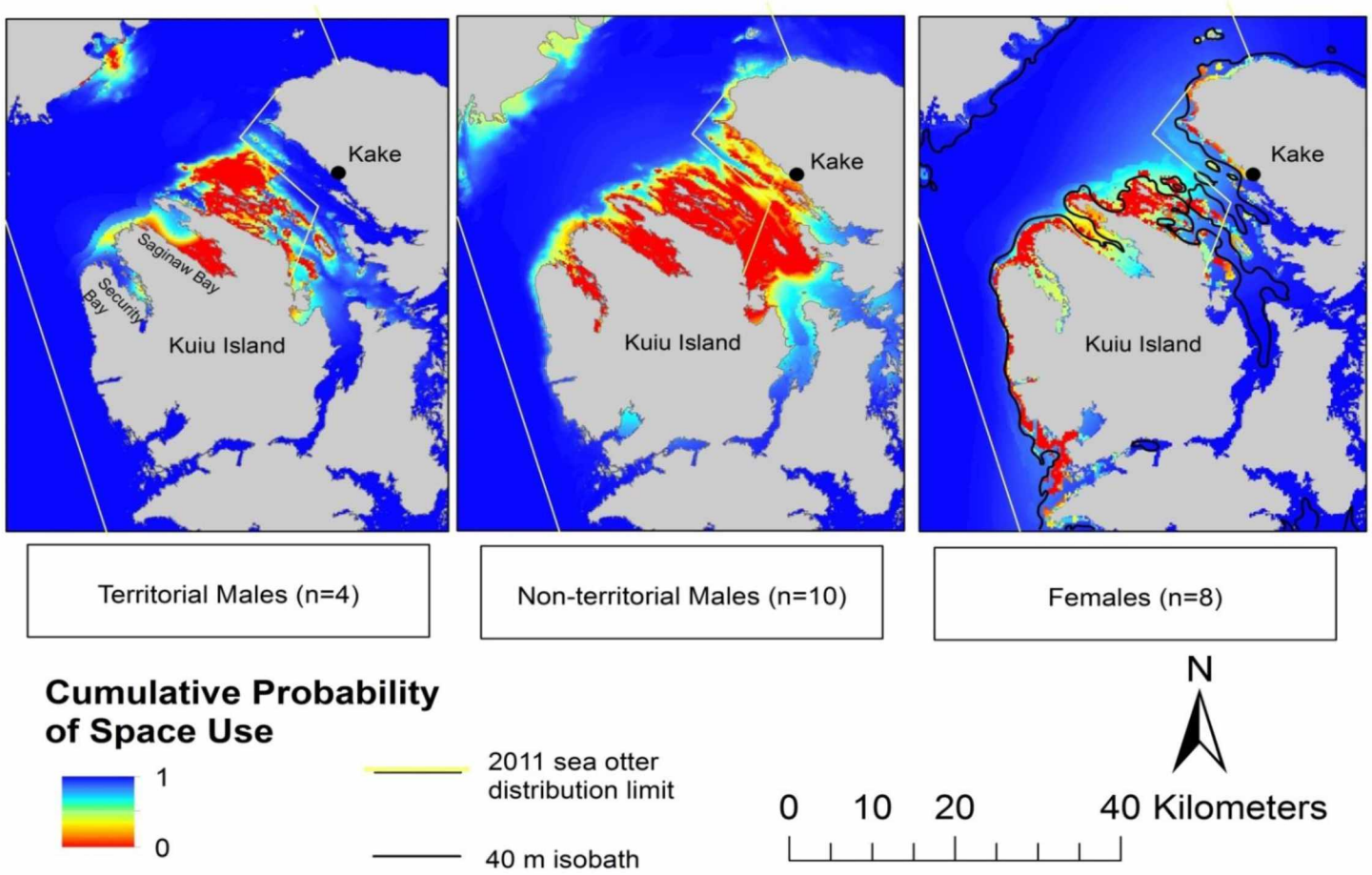

Figure 2.4 Cumulative probability distributions of space use for territorial males, non-territorial males and females calculated using the model average of individual level best fit. The surveyed distribution of sea otters in the study site from a 2011 population survey effort is depicted on each map and the 40 m isobaths on the panel representing females.

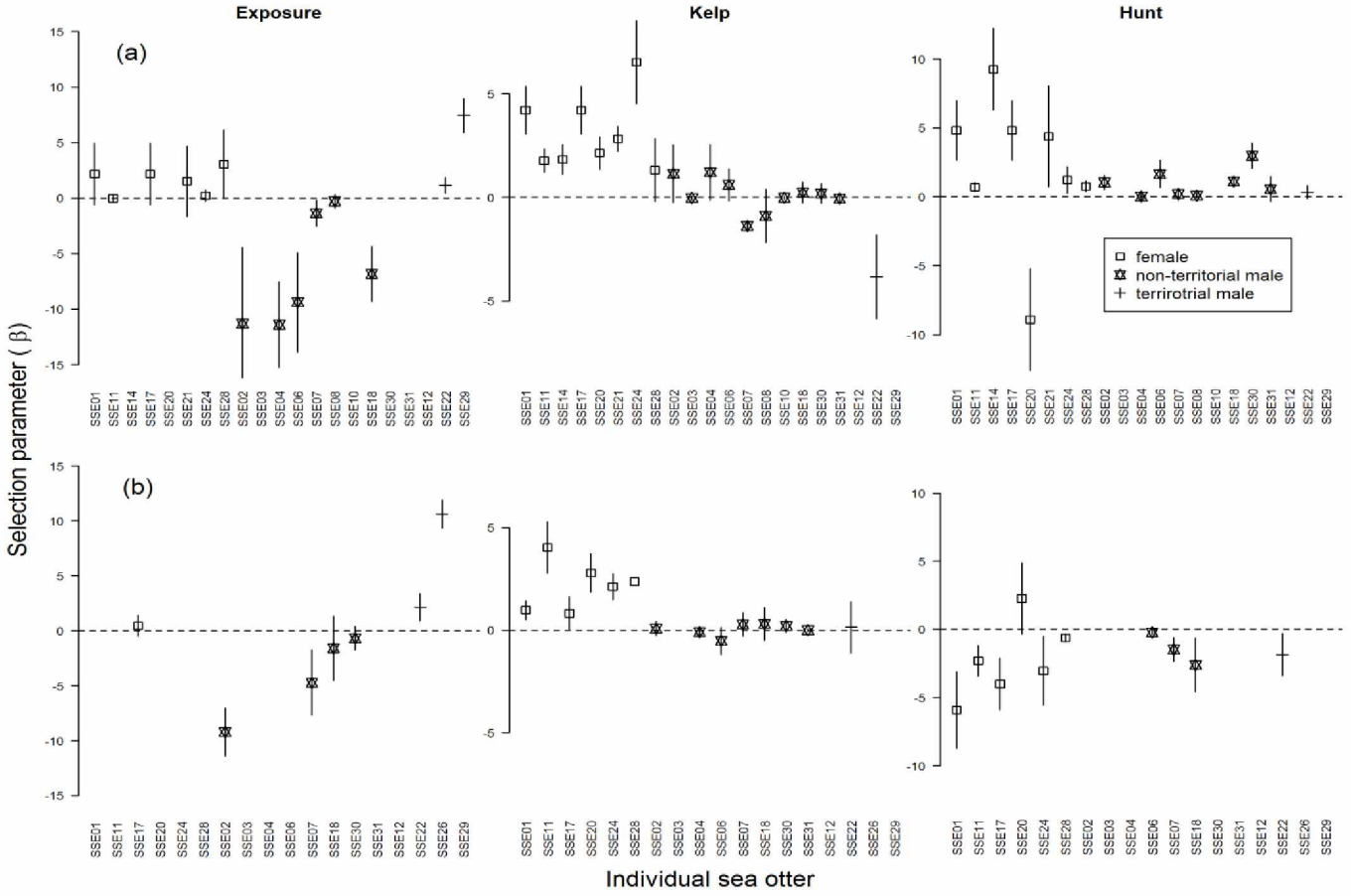

Figure 2.5 Standardized selection coefficients during (a) pre- and (b) post-hunting periods for females, non-territorial males and territorial males for exposure, hunting and kelp covariates. Points, axes and coefficients as in Figure 2.

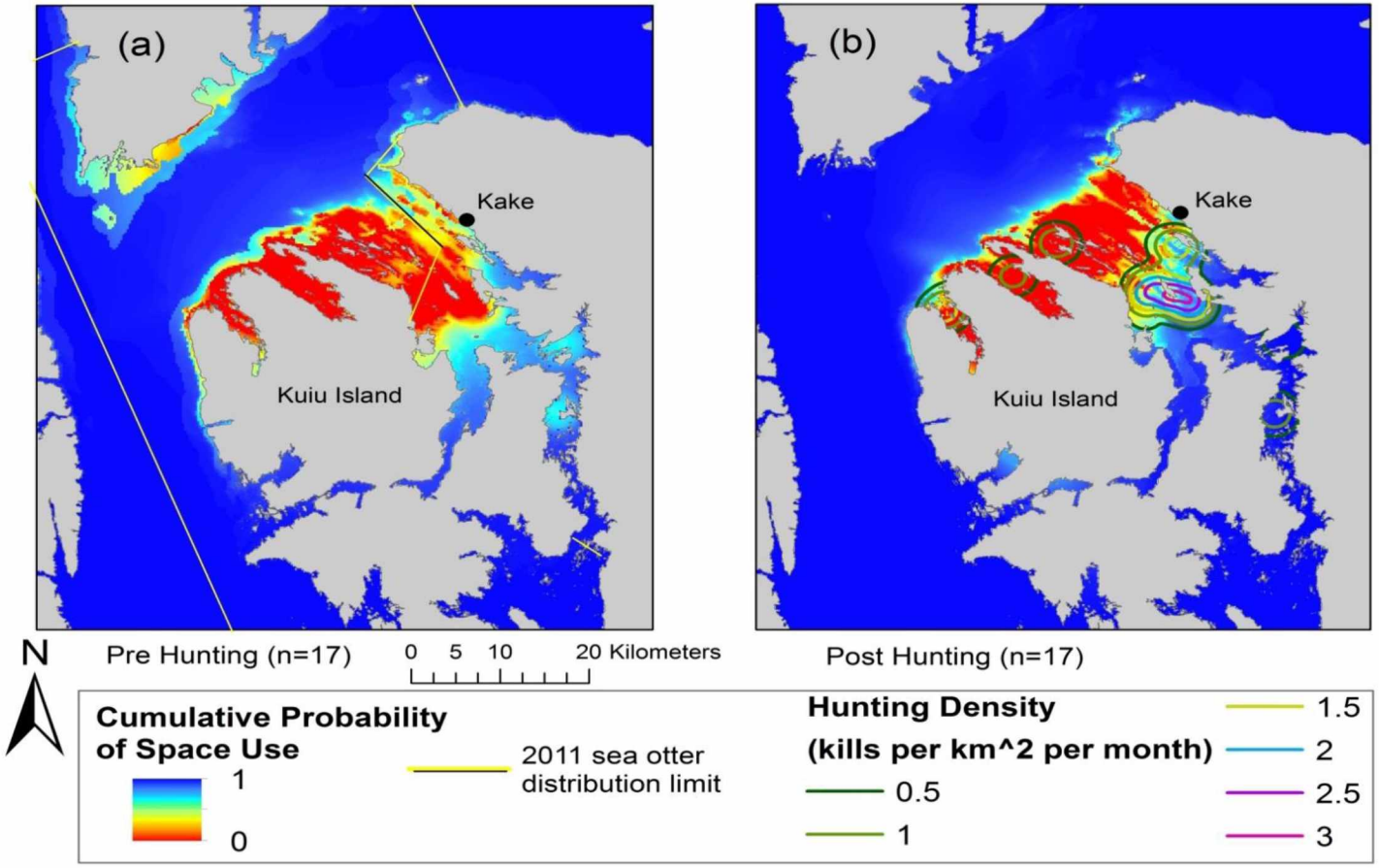

Figure 2.6 Cumulative probability distributions of space use for (a) pre- and (b) post-hunting periods calculated using the model average of individual level best fits. The surveyed distribution of sea otters in the study site from a 2011 aerial survey is the yellow line in (a) and the density of hunting -related mortality on sea otters taken in 2012 and 2013 is shown in (b).

Appendix 2.A Supplemental material, spatial modeling variables and results

Table 2.A-1 *A priori* candidate models used to estimate sea otter space use in Southeast, Alaska. The table includes the number of telemetry locations (n), estimated age assessed by tooth cementum at capture, number of estimated model parameters (K), the difference between each model and the model with the lowest AIC_c for each model set (ΔAIC_c), and the Akaike weight (w_i). Only models that have w_i greater than 0.05 are presented.

Individual	Age	Model[a]	K	ΔAIC_c	w_i
Females					
Otter 1 (n=39)	NA	KELP+HUNT+DIST	8	0.00	0.4175
		EXP+KELP+HUNT+DIST	9	1.11	0.2900
		KELP+HUNT	7	1.38	0.2590
Otter 11 (n=39)	NA	KELP+DIST	7	0.00	0.3121
		KELP+HUNT+DIST	8	0.36	0.2267
		BATHY +KELP	8	0.38	0.2254
		EXP+KELP+HUNT+DIST	9	0.40	0.1740
Otter 14 (n=39)	2	BATHY+KELP+HUNT	9	0.00	0.5367
		BATHY+KELP+DIST	9	2.07	0.1910
		KELP+HUNT	7	2.11	0.1868
Otter 17 (n=39)	4	KELP+DIST	7	0.00	0.7815
		EXP+KELP	7	4.41	0.0862
Otter 20 (n=38)	3	KELP	6	0.00	0.2846
		BATHY+KELP	8	0.90	0.1813
		KELP+DIST	7	1.47	0.1367
		EXP+KELP	7	1.69	0.1223
Otter 21 (n=20)	7	KELP+HUNT+DIST	8	0.00	0.5005
		EXP+KELP+HUNT+DIST	9	1.25	0.2671
		KELP+DIST	7	1.55	0.2302
Otter 24 (n=39)	8	KELP	6	0.00	0.5246
		KELP+HUNT	7	2.07	0.2745
		BATHY+ KELP+HUNT	9	2.11	0.0950
Otter 28 (n=34)	3	BATHY+KELP	8	0.00	0.3698
		BATHY+KELP+HUNT	9	1.40	0.1839
		KELP+DIST	7	1.94	0.1400
		EXP+KELP+HUNT+DIST	9	2.65	0.0982
		KELP+HUNT+DIST	8	3.42	0.0668
Territorial Males					
Otter 12 (n=46)	7	BATHY+DIST	8	0	0.961
Otter 22 (n=31)	8	BATHY+KELP+HUNT	9	0	0.3411
		EXP+KELP+HUNT+DIST	9	0.45	0.2732
		BATHY+DIST	8	1.23	0.1700
		KELP+HUNT+DIST	8	2.9	0.0911

Table 2.A-1 continued

Otter 26 (n=20)	7	EXP	6	0	0.9998
Otter 29 (n=41)	7	BATHY	7	0	1
Non-Territorial Males					
Otter 2 (n=36)	4	EXP	6	0	0.6936
		EXP+KELP	7	1.96	0.2609
Otter 3 (n=38)	2	BATHY	7	0	0.3405
		BATHY+STRA	8	0.12	0.3199
		BATHY+KELP	8	1.65	0.1492
		BATHY+DIST	8	1.99	0.1261
		BATHY+KELP+HUNT	9	3.71	0.0533
Otter 4 (n=34)	1	EXP	6	0	0.3896
		EXP+KELP	7	0.96	0.2346
		BATHY +KELP	8	1.53	0.1863
		BATHY +KELP+HUNT	9	1.95	0.1429
Otter 6 (n=38)	1	BATHY +STRA	8	0	0.4603
		BATHY +KELP	8	1.38	0.2304
		EXP	6	2.98	0.1036
		BATHY +KELP+HUNT	9	3.43	0.0828
		EXP+KELP	7	4.25	0.0549
Otter 7 (n=38)	2	EXP	6	0	0.9678
Otter 8 (n=18)	7	EXP+KELP+HUNT+DIST	9	0	0.5215
		KELP+HUNT+DIST	8	0.7	0.3356
Otter 10 (n=24)	7	BATHY	7	0	0.3942
		BATHY+KELP	8	1.96	0.3341
		BATHY+DIST	8	2.05	0.2111
Otter 18 (n=37)	7	EXP+KELP+HUNT+DIST	9	0	0.9865
Otter 30 (n=32)	4	BATHY +KELP+HUNT	9	0.33	0.1745
		KELP+HUNT+DIST	8	0.51	0.1637
		BATHY	7	0.7	0.1036
		BATHY +KELP	8	1.02	0.0883
		KELP+DIST	7	1.3	0.0765
Otter 31 (n=36)	2	BATHY+DIST	8	0	0.5122
		BATHY+KELP	8	1.05	0.2991
		BATHY	7	1.9	0.1612

[a]Each candidate model refers to the NULL model which refers to the bivariate normal distribution in conjunction with the terrestrial (LAND) covariate that was not estimated, but held constant and included as the null model; the null model has five estimated parameters μ_x, μ_y, σ_x, σ_y and ρ (see equation 1); BATHY is a continuous covariate defining the tide corrected depth represented by both a linear and quadratic term; EXP is a categorical covariate defining the exposure of an area; KELP is a categorical covariate defining the presence of canopy kelps within the study area; HUNT is a continuous variable defining the density of legal subsistence takes of sea otters within the study site; and DIST is a continuous covariate defining the distance to the nearest shoreline. NA refers to sea otters not aged because a pre-molar tooth was not collected at capture.

Table 2.A-2 Variables used to model the space use of sea otter in Southeast Alaska.

Variable	Variable Type	Description	Source
Terrestrial Habitat (LAND)	binary (0=land, 1=marine)	Generated using the USGS shoreline coverage p4. This variable was not estimated rather the selection parameter remained fixed at -1 (no selection) where terrestrial habitats are present.	USGS National Hydrography Dataset http://nhd.usgs.gov/
Bathymetry (BATHY)	continuous	Generated from NOAA bathymetry data	NOAA National Geophysical Data Center http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html
Bathymetry^2 (BATHY^2)	continuous	Generated from NOAA bathymetry data.	NOAA National Geophysical Data Center http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html
Exposure (EXP)	categorical	Generated using climate/wind speed data from the Kake, Alaska airport and the ARCGIS WAVE Tool (ARCGIS, Redland, CA)	Climate data was recorded at Kake, AK and obtained from NOAA National Climatic Data Center http://www.ncdc.noaa.gov/cdo-web/
Canopy Kelp Coverage (KELP)	categorical	Generated using a base map and categorical variables developed by ShoreZone, a two- dimensional map was then digitized from aerial survey mapping and photography conducted during winter and summer months 2012-14.	A base map of one dimensional canopy kelp coverage was obtained from Shorezone https://alaskafisheries.noaa.gov/shorezone/.
Distance to Shore (DIST)	continuous	Generated using the Distance toolset in ARCGIS, (Redland, CA). Represents Euclidian distance from the grid midpoint to the nearest terrestrial habitat.	USGS National Hydrography Dataset http://nhd.usgs.gov/
Hunting Density (HUNT)	continuous	Generated using a kernel density estimator in ARCGIS, (Redland, CA), of spatially explicit USFWS sea otter marking and tagging records.	US Fish and Wildlife Service, Marine Mammal Management office, Anchorage, Alaska.

Table 2.A-3 *A priori* candidate models used to estimate sea otters space use in Southeast, Alaska during pre- and post-hunting periods (May 11, 2011 to September 30, 2012 and October 1, 2012 to May 1, 2014, respectively). The table includes the number of telemetry locations (n), number of estimated model parameters (K), the difference between each model and the model with the lowest AIC_c for each model set (ΔAIC_c), and the Akaike weight (w_i). Only models that have w_i greater than 0.05 are presented.

Individual	Model[a]	K	ΔAIC_c	w_i
Females				
Pre-hunt				
Otter 1 (n=18)	KELP+HUNT+DIST	8	0.00	0.4175
	EXP+KELP+HUNT+DIST	9	1.11	0.2900
	KELP+HUNT	7	1.38	0.2590
Otter 11 (n=23)	KELP+DIST	7	0.00	0.3456
	KELP+HUNT	7	0.11	0.2801
	KELP	6	0.56	0.1602
	KELP+HUNT+DIST	8	1.04	0.1333
Otter 14 (n=21)	BATHY+KELP+HUNT	9	0.00	0.4943
	KELP+HUNT	7	1.34	0.2711
	KELP+HUNT+DIST	8	2.21	0.1931
Otter 17 (n=21)	EXP+KELP	7	0.00	0.8391
	EXP+KELP+HUNT+DIST	9	3.53	0.1235
Otter 20 (n=19)	BATHY+KELP+HUNT	9	0.00	0.8500
	KELP+HUNT	7	5.74	0.0500
Otter 21 (n=20)	KELP+HUNT+DIST	8	0.00	0.5976
	EXP+KELP+HUNT+DIST	9	1.26	0.2711
Otter 24 (n=15)	KELP	6	0.00	0.5246
	KELP+HUNT	7	0.49	0.2745
	EXP+KELP	7	1.55	0.1100
	KELP+DIST	7	2.05	0.0953
Otter 28 (n=18)	EXP+KELP	7	0.00	0.3966
	KELP	6	1.57	0.1814
	EXP+KELP+HUNT+DIST	9	1.92	0.1523
	KELP+HUNT	7	2.85	0.1134
Post-hunt				
Otter 1 (n=21)	BATHY+KELP+HUNT	9	0.00	0.3780
	KELP+HUNT	7	0.10	0.2924
	KELP+HUNT+DIST	8	1.82	0.1241
Otter 11 (n=16)	BATHY+KELP	8	0.00	0.4537
	KELP	6	1.26	0.2279
	BATHY+KELP+HUNT	9	1.92	0.1276
	KELP+DIST	7	1.96	0.1255
Otter 17 (n=18)	BATHY+KELP	8	0.00	0.2805
	KELP	6	0.82	0.1861

Table 2.A-3 continued

	BATHY+KELP+HUNT	9	1.46	0.1354
	EXP+KELP	7	1.64	0.1236
	KELP+HUNT	7	1.77	0.1157
	KELP+DIST	7	2.26	0.0904
Otter 20 (n=19)	KELP+HUNT	7	0.00	0.5664
	KELP+DIST	7	3.13	0.1187
	KELP+HUNT+DIST	8	3.24	0.1121
	BATHY+KELP+HUNT	9	3.65	0.0914
Otter 24 (n=24)	BATHY+KELP	8	0.00	0.5310
	BATHY+KELP+HUNT	9	0.44	0.4253
Otter 28 (n=16)	BATHY+KELP	8	0.00	0.3670
	BATHY+KELP+HUNT	9	0.87	0.2627
	KELP+DIST	7	1.23	0.2144
	KELP	6	1.74	0.1117
Territorial Males				
Pre-hunt				
Otter 12 (n=22)	BATHY+DIST	8	0	0.9511
Otter 22 (n=16)	BATHY+KELP+HUNT	9	0	0.3652
	BATHY+DIST	9	0.45	0.211
	BATHY	7	1.23	0.2034
Otter 29 (n=21)	BATHY	7	0	0.9999
Post-hunt				
Otter 12 (n=24)	BATHY+DIST	8	0	0.9456
	BATHY	8	6.27	0.0338
Otter 22 (n=15)	BATHY+KELP+HUNT	9	0	0.3782
	EXP+KELP+HUNT+DIST	9	0.15	0.2151
	BATHY+DIST	7	0.43	0.2045
	KELP+HUNT+DIST	8	1.40	0.1432
Otter 26 (n=20)	EXP	6	0	0.9998
Otter 29 (n=20)	BATHY	8	0	0.9611
Non-Territorial Males				
Pre-hunting				
Otter 2 (n=20)	EXP+KELP+HUNT+DIST	9	0.00	0.5812
	EXP	6	1.36	0.2935
	BATHY+DIST	8	2.60	0.0613
Otter 3 (n=16)	BATHY	7	0.00	0.4382
	BATHY+KELP	8	1.02	0.2910
Otter 4 (n=19)	EXP+KELP	7	0.00	0.4301
	EXP	6	0.21	0.3873
	EXP+KELP+HUNT+DIST	9	2.24	0.1403

Table 2.A-3 continued

Otter 6 (n=18)	EXP+KELP+HUNT+DIST	9	0.00	0.4396
	EXP	6	0.96	0.2715
	EXP+KELP	7	1.37	0.2211
Otter 7 (n=18)	BATHY+DIST	8	0.00	0.5811
	EXP	6	3.73	0.0898
	EXP+KELP+HUNT+DIST	9	4.15	0.0729
Otter 8 (n=15)	KELP	6	0.00	0.2985
	EXP	6	1.08	0.1924
	KELP+HUNT	7	1.39	0.1289
	EXP+KELP	7	1.44	0.1261
	KELP+DIST	7	1.61	0.0707
	HUNT	8	1.97	0.0592
	BATHY+KELP	8	2.00	0.0582
Otter 10 (n=21)	BATHY	7	0.00	0.4984
	BATHY+DIST	8	2.02	0.1150
	BATHY+KELP	8	2.04	0.1111
Otter 18 (n=21)	EXP	6	0.00	0.6283
	EXP+KELP	7	1.66	0.2744
	EXP+KELP+HUNT+DIST	9	4.41	0.0693
Otter 30 (n=16)	BATHY+KELP+HUNT	9	0.00	0.4219
	HUNT	8	0.84	0.3162
	KELP+HUNT	7	1.54	0.1492
Otter 31 (n=16)	BATHY+DIST	8	0.00	0.5348
	BATHY	7	2.05	0.1633
	BATHY+KELP+HUNT	9	2.97	0.1030
Post-hunting				
Otter 2 (n=16)	EXP	6	0.00	0.7032
	EXP+KELP	7	1.77	0.2522
Otter 3 (n=22)	BATHY	7	0.00	0.8251
	BATHY+DIST	8	3.24	0.1148
Otter 4 (n=15)	BATHY	7	0.00	0.8136
Otter 6 (n=20)	BATHY	7	0.00	0.7682
Otter 7 (n=20)	EXP	6	0.00	0.3976
	EXP+KELP	7	0.25	0.3342
	EXP+KELP+HUNT+DIST	9	1.71	0.1225
Otter 18 (n=16)	DIST	7	0.00	0.4314
	BATHY+DIST	8	1.06	0.2541
	KELP+DIST	7	1.93	0.1646
	EXP+KELP+HUNT+DIST	9	2.36	0.1323
Otter 30 (n=16)	EXP	6	0.00	0.4024
	KELP	6	1.06	0.1480
	EXP+KELP	7	1.50	0.0966

Table 2.A-3 continued

	DIST	6	1.30	0.0857
Otter 31 (n=20)	BATHY	7	0.00	0.9689

[a]Each canidate model refers to the bivariate normal distribution in conjunction with the terrestrial (LAND) covariate that was not estimated, but held constant and included as the null model; the null model has five estimated parameters μ_x, μ_y, σ_x, σ_y and ρ (see equation 1); BATHY is a continuous covariate defining the tide corrected depth represented by both a linear and quadratic term; EXP is a categorical covariate defining the exposure of an area; KELP is a categorical covariate defining the presence of canopy kelps within the study area; HUNT is a continuous variable defining the density of legal subsistence takes of sea otters within the study site; and DIST is a continuous covariate defining the distance to the nearest shoreline.

Chapter 3: Recolonization and forage ecology of sea otters (*Enhydra lutris*) in southern Southeast Alaska[3]

Abstract

Recolonization and subsequent population expansion of a predator will invoke major shifts in community structure and dynamics of prey resources. Ecological theory suggests diet diversity and ecosystem stability will increase as persistence of the predator increases and preferred prey resources are reduced. The sea otter population in southern Southeast Alaska has grown exponentially to 13,139 (cv = 0.17) individuals in 2011, with an annual growth rate of 12% since the introduction of 106 individuals in 1968. We assessed the diet of sea otters in southern Southeast Alaska by observing 7,587 individual foraging dives between June 2011 and May 2013 from a range of habitats (i.e. soft substrate, rocky reefs, kelp forests) and locations with varying duration of sea otter presence. Sea otters in our study area consumed a total of 73 unique prey types grouped into 19 prey categories. Sea otter diet diversity (Shannon-Wiener *H'*) increased log-linearly with duration of sea otter presence. In the original translocation areas sea otters exhibited the greatest diet diversity; while in areas that were only recently colonized, sea otters had less diverse diets. Forty-six percent of the diet at the population level represented commercially important prey. When sea otters first colonize an area, red sea urchins *Strongylocentrotus franciscanus* and Dungeness crab *Metacarcinus magister* are more common in the diet. The proportion of the diet of commercial fisheries species decreased as observed

[3] Hoyt, Z.N., M.T. Tinker, V.A. Gill, A. Rice, G. L. Eckert. Prepared for submission in Marine Ecology Progress Series.

maximum sea otter density increased, suggesting depletion of commercial prey species. Factors that significantly described prey composition included distance from release site and exposure. The sea otter population will likely continue to grow and consume commercially important prey as they continue to colonize Southeast Alaska.

Keywords

Diet diversity, reintroduction, fisheries conflict, predator, shellfish, marine mammal

Introduction

When the density of an apex predator increases, the state of the ecosystem can be altered, as evident by changes in prey assemblages and/or vegetation (Estes and Palmisano 1974, Ripple and Beschta 2012, Stevenson et al. 2007). Many marine mammals are apex predators that remove substantial biomass and structure communities and ecosystems (Estes et al. 2011, Ripple et al. 2014, Terborgh et al. 2010). Marine predators are often tightly coupled to the spatial distribution and abundance of their prey (Benoit-Bird et al. 2013). When marine mammal prey is commercially important, conflicts may result between humans and the predators. Extirpation and reintroduction of predators can reveal trophic interactions and resulting changes in ecosystem states (Beschta and Ripple 2009, Ripple et al. 2014).

Marine mammal populations have been reduced by harvest for their fur, oil, food or as competitors for prey resources, resulting in ecosystem changes throughout the world (Estes et al. 2006, Springer et al. 2003). In certain instances the reduction of top trophic predators has led to increased mesopredators and prey assemblages (Estes et al. 2009), which have been targeted by humans due to their increased abundance (Bowen 1997). As marine mammals have increased in number due to protection from human exploitation and conservation efforts, the impacts on fisheries resources are being realized. Often the less diverse ecosystem state without top trophic levels becomes culturally accepted because of the great commercial fisheries potential (Jackson et al. 2001, Sáenz-Arroyo et al. 2005) .

Diet diversification may play an important role in predator prey interactions as marine mammal populations recover. In order for habitats to sustain marine mammals for long durations, given their high energetic needs and the vulnerability of their prey, diets may shift as resources are locally depleted (Trites et al. 1997). This is an important element of optimal foraging theory, which states that optimally foraging animals may include a greater range of prey items in their diets if the density of preferred prey items decreases over time (Schoener 1971). More specifically, as preferred prey density decreases, the mean search time increases and thereby makes it less profitable to overlook lower value prey items (Ostfeld 1982).

Sea otters provide a unique opportunity to directly observe diet and therefore quantify the direct impacts of a top marine mammal predator on prey diversity and fisheries resources with few assumptions. Sea otters are relatively sedentary, forage nearshore, and consume their prey at the surface where they can be directly observed (Riedman and Estes 1990). Further, sea otters are a keystone species and an apex predator, and as such, have a profound impact on nearshore ecosystems. Additionally, sea otters are thought to forage optimally, selecting resources that offer the highest rates of energy return given their size, abundance, ease of acquisition, and caloric content (Ostfeld 1982). In a eutrophic estuary in central California, sea otter predation on small crabs led to a trophic cascade, in which mesograzers increased, leading to increased grazing pressure on algae epiphytes, which increased the abundance and health of eelgrass (Hughes et al. 2013). Increases in sea otter density within the estuary corresponded to increases in eelgrass cover since sea otter colonization in 1984 (Hughes et al. 2013). Sea otters are also well known for their role in structuring kelp forests by removal of herbivores, predominantly their preferred prey, sea urchins (Estes and Duggins 1995, Estes and Palmisano 1974, Ostfeld

1982). The large consumption potential of sea otters has also led to reduction in commercially important shellfish. Sea otters likely limited the Dungeness crab *Metacarcinus magister* fishery in Prince William Sound (Garshelis and Garshelis 1984), have reduced the sea cucumber *Parastichopus californicus* fishery in Southeast Alaska (Larson et al. 2013) and the potential for geoduck clam *Panopea generosa* fisheries in British Columbia (Reidy 2011); however, direct impacts have been difficult to quantify (Carswell et al. 2015, Estes and VanBlaricom 1985). Excluding Glacier Bay only minimal effort has been undertaken to understand the recolonization and impacts of sea otters on the nearshore ecosystem of Southeast Alaska (Kvitek et al. 1993, Kvitek et al. 1992). In Glacier Bay rapid colonization by sea otters reduced the size and density of clams (Weitzman 2013) and in nearby Dundas Bay excluded Dungeness crab commercial fishing (Shirley et al. 1996).

Commercially important prey items of sea otters are typically large and calorically rich. Further, a few of these species such as red sea urchins *Strongylocentrotus franciscanus*, Dungeness crab, sea cucumbers and pinto abalone *Haliotis kamtschatkana* are easy to capture and typically have short handling times when preyed upon by sea otters (Oftedal et al. 2007). Others such as geoduck clams are energetically demanding to capture but are typically large and calorically rich (Kvitek et al. 1993). Optimal foraging theory states that animals broaden their diets to include more low value species over time after being introduced into an area (Schoener 1971). Foraging effort has been found to increase and energy acquisition rates decrease as sea otter populations reach equilibrium densities (Estes et al. 1982, Estes et al. 1986, Garshelis et al. 1986, Watt et al. 2000).

Sea otters were systematically removed in the northeast Pacific in the early 1800s by the fur trade and were functionally extinct in Southeast Alaska by the 1850s (Personal Communication, Katrina Wessels). Sea otters were granted protection throughout their range by an international treaty in 1911 (Kenyon 1969). Subsequently, sea otters were successfully reintroduced to Southeast Alaska beginning in 1965 from 411 individuals translocated to six sites from remnant populations at Amchitka Island and Prince William Sound (Burris and McKnight 1973). With a population growth potential (R_{max}) of 20%, the reintroduced population has expanded (Estes 1990). Populations of sea otters in Alaska have experienced differences in population trajectories. For example a population in Kachemack Bay increased between 2002-08 by 28% annually, exceeding R_{max}, suggesting immigration from adjacent populations, while the remnant population in western Prince William Sound experienced a 3% growth rate between 1993-2009 following a catastrophic oil spill in 1988 (Bodkin et al. 2011). In contrast, the population in the Aleutian Islands declined by 70% between 1992 and 2000 and showed continued evidence of decline until at least 2003 (Doroff et al. 2003, Estes et al. 2005). In Glacier Bay, a recently de-glaciated fjord in northern Southeast Alaska, sea otter populations have increased rapidly after first colonizing the bay in 1995 to some of the highest known densities of sea otters throughout their range, with nearly 8500 individuals estimated inhabiting the bay in 2012 (Weitzman 2013). The demographics of sea otters vary in Southeast Alaska, with certain areas being colonized for extended times at varying densities, while other areas have only recently been colonized as the population continues to grow. For example, Coronation Island, an area first colonized by sea otters by 1975, experienced a maximum observed density of 5.3 sea otters per km^2 in 1988 and has experienced a reduction in density ever since. In 2010 the density was measured at 0.4 sea otter per km^2 (Pitcher 1989, USFWS 2014).

Here we quantified the diet and demographics of sea otters in southern Southeast Alaska to better understand the direct impacts of sea otters on prey resources, particularly commercially important invertebrates. We summarized the abundance, distribution and local density of the population and then tested if the diet of sea otters differed geographically. Then we related sea otter diet to demographics including (1) persistence or how long sea otter have occupied an area, (2) local density, (3) distance from release sites, (4) and geographic location.

Methods

Study area and sea otter demographics

The study was conducted in southern Southeast Alaska between Frederick Sound (57.1^{0}N, 134.6^{0}W) and Dixon Entrance (54.6^{0}N, 132.7^{0}W; Figure 3.1) in the eastern Pacific Ocean. We calculated the density of sea otters on small spatial scales (45 - 172 km^2), referred to as foraging regions henceforth, for each survey effort between 1975 and 2011, using survey data and a digital coverage of sea otter habitat with bathymetry < 60 m depth (Figure 3.1). Additionally, we defined the exposure category of foraging regions as: (1) exposed, (2) coastal or (3) protected, in relation to the exposure to the Pacific Ocean and Frederick Sound (the largest body of water in Southeast Alaska), defined by wave energy observations during data collection and information from aerial imagery in Shorezone (Figure 3.1; Harney et al. 2008). Further, we established a geospatial distribution of sea otters over time within our study area since reintroduction; we refer to this as persistence. Persistence represents the spatial gradient in which sea otters colonized southern Southeast Alaska. Each forage region was given a persistence value (year of known sea

otter colonization) as a space-for-time substitute as sea otter surveys were not conducted regularly within the study area. Least cost distance (as the sea otter swims) was derived from the geographic centroid of each foraging region to the nearest release site using methods presented in Ray (2005).

Foraging observations

Foraging observations, including behavioral parameters and diet composition, were collected using standardized methods from observing individual sea otters (Tinker et al. 2008, Watt et al. 2000). Shore-based observations were made from southern Admiralty Island to Cape Chacon between June 2011 and May 2013 (Figure 3.1). Locations were representative of southern Southeast Alaska and varied in habitat type, sea otter persistence, density and distance from release site. Questar field telescopes (Isantic, MN) and binoculars were used to observe sea otters and identify prey. Foraging dives of individual sea otters were recorded as successful or unsuccessful. For successful dives, dive times and surface intervals between dives were recorded, prey were identified to the lowest possible taxon, foraging locations were marked using GPS, and the date and time of the observation recorded. The size of the prey was estimated by each observer as a proportion of the sea otter's paw size. The number of prey items were recorded as sea otters will often capture multiple prey items during a successful dive. Finally, we collected successive dives from an individual continuously foraging, which we refer to as a foraging bout. Researchers observed an individual sea otter until it had either stopped foraging, 20 foraging dives had been observed, or it was lost from view. If two bouts were recorded from one location the observers would actively change observation location to geographically distribute and reduce bias of the observation data.

Prey types were sampled from the study area to estimate edible biomass consumed and biomass intake rate for each prey type and size using a variety of techniques including SCUBA, intertidal sampling and trapping. The wet edible biomass (i.e. excluding shells, urchin spines and inedible parts) and lengths of each prey were recorded to provide estimates of edible biomass for each prey type available to a sea otter. We attempted to collect a range of sizes for each prey type and used standardized procedures reported by Oftedal et al. (2007) to assure we had reasonable estimates for a range of sizes for each prey item. When we were not able to collect a particular prey type or size, we used prey biomass-size relationships collected from nearby sea otter prey populations in Alaska (Glacier Bay and Prince William Sound) and reported by Oftedal et al. (2007).

Diet analyses

The relative frequency of capture and consumption of each prey type was used to calculate diet composition (in terms of biomass) at three spatial scales including: 1) foraging regions used in calculating sea otter density, 2) sea otter persistence categories and 3) the population level. Because sea otters prey upon varying prey types and sizes, and field conditions can be challenging it is not always possible to reliably identify every prey item, leading to observations categorized as unknowns. Therefore, to obtain measures of prey contribution to the diet, we incorporated biomass-size relationships and associated uncertainty (*SD*) into a Monte Carlo bootstrap procedure (Tinker et al. 2012). This procedure served to incorporate uncertainty and adjust for several known biases associated with shore-based observations of sea otter diets and is fully described by Tinker et al. (2012). This bootstrap procedure allowed us to estimate means,

standard deviations and confidence intervals for the proportion by weight of each prey item in the diet. We square root transformed diet composition data to reduce the influence of large values. Prey types were grouped into taxonomically or morphologically similar categories to simplify interpretation of the results.

To determine if the diet composition of sea otters differed between foraging regions, we employed both univariate and multivariate approaches. Using a permutation based multivariate analysis (PerMANOVA), developed and reported by Anderson (2001), we tested for differences in diet composition (in units of biomass) among foraging regions that had different levels of exposure and sea otter persistence. We ran 5000 permutations within the PerMANOVA framework to estimate the probability (p-value) that observed differences are due to chance, given the null hypothesis of no differences in diet composition. Diet similarities between each pair of foraging regions were calculated using a Bray-Curtis dissimilarity measure of distance (Clarke et al. 2006). Because PerMANOVA analyses are sensitive to multivariate spread, we tested for multivariate dispersion of diet composition of foraging regions for our different levels of exposure and persistence individually (Anderson 2006). Additionally, we conducted a similarity percentage analysis (SIMPER) to determine what prey species contributes more to the explained variance in the PerMANOVA analysis (Clarke and Warwick 2001). To visualize the prey composition of sea otters, we employed a non-metric multidimensional scaling ordination (nMDS) and assessed whether the following variables were significantly related to the ordination axes using four individual permutation-based vector fitting regressions for: (1) least cost distance from release site, (2) latitude, (3) longitude, (4) persistence, and (5) maximum sea otter density (McCune and Grace 2002) .

We examined the diet diversity at the sea otter persistence scale using the Shannon-Wiener diversity index (*H'*) (Shannon and Weaver 1949). We investigated the relationship between: (1) maximum sea otter density observed from all sea otter survey efforts (1975-2010) and the commercial contribution to sea otter diet by foraging region and (2) sea otter persistence and diet diversity in each foraging region using linear regression. We hypothesized that both relationships would follow a log-linear trend as sea otter are known to have dynamic impacts on nearshore ecosystems before a stable ecological state is reached (Estes and Palmisano 1974, Simenstad et al. 1978). All analysis were completed using R version 3.0.2 (R Development Core Team 2010) while spatial parameters were derived and mapped in ARCGIS 10.1 (ESRI 2012).

Results

The sea otter population in southern Southeast Alaska has grown exponentially in terms of both population (12% per year since the reintroduction of 106 individuals in 1968, Figure 3.2) and area occupied (9% per year, $R^2 = 0.99$, $F_{(1,5)} = 440.4$, $p < 0.001$, Figure 3.1). Further, a linear relationship between the square root of area < 60 m in depth colonized by sea otters for the southern Southeast Alaska sea otter population indicates the population has increased radially at 1.42 km y^{-1} ($R^2 = 0.97$, $F_{(1,5)} = 43.01$, $p = 0.001$; Figure 3.3), assuming a 12% growth rate and that colonization occurs as a diffusion process. However, at the foraging region scale density dependence was observed at regions colonized for > 35 years as the density of sea otters remained stable or decreased between surveys conducted in the 1980s and those conducted in the 2000s. The average rate of increase was slightly lower in terms of area occupied (9%) than for

population growth (12%), supporting the concept of density dependence within at least some regions.

Observations on 7,587 individual foraging dives, representing 699 foraging bouts, revealed that sea otters in our study area consumed a total of 73 unique prey types grouped into 19 prey categories (Figure 3.4). The most common prey items (by biomass) were red sea urchins followed by clams, and the least consumed prey item was pinto abalone (Figure 3.4a). Six commercially important species were sea otter prey within our study area, including Dungeness crab, California sea cucumber, geoduck clams, red sea urchins, pinto abalone and red king crab *Paralithodes camtschaticus*, and represented 46% (± 6% SD) of the overall diet. We should clarify that several species of shrimp are commercially harvested in Southeast Alaska; however, we were generally unable to identify shrimp to the species level during observations. Further the prevalence of shrimp in the overall diet was low (< 1%) suggesting that the contribution of commercially important shrimp species to the diet of sea otters was minor. The biomass intake rate for each prey grouping at the population scale is reported in Figure 3.A-1.

Sea otters consumed the highest proportion of commercially important species in recently colonized areas (since 2010) and where the maximum density of sea otters was the smallest since reintroduction (Figure 3.5). In recently colonized areas (since 2010) the proportion of the diet represented by commercially important species was greatest (63% ± 9% SD) compared to areas where sea otters have persisted for periods greater than 40 years (< 38%; Figure 3.4). The commercial component of the diet for areas where sea otter have persisted for 10 - 40 years was similar and averaged 27% (± 6% SD). When individual commercial prey species were examined,

sea otters consumed greater proportions of both red sea urchins and Dungeness crab in areas recently colonized or having low persistence (i.e. the proportional discrepancy from the population level mean was positive, Figure 3.4b-h); however, the same trend was not observed for geoduck clams or California sea cucumbers as they represented a much lower percentage of the diet and the proportional discrepancy from the population level mean by persistence level was variable (Figure 3.4). Pinto abalone and red king crab were not prevalent prey items in southern Southeast Alaska, both representing < 0.5% of the overall diet (Figure 3.4). The proportion of the sea otter diet that was commercially important appeared to be influenced by the maximum observed density of sea otters, as foraging regions that experienced a high maximum observed density of sea otters had a low commercially important prey component ($R^2 = 0.45$, $F_{(1,15)} = 12.5$, $p = 0.003$; Figure 3.5). Three other non-commercial prey groups appeared to be targeted by sea otters, including clams (22% of overall diet), sea urchins (predominantly green sea urchins *Strongylocentrotus droebachiensis*, 10% of overall diet) and non-commercial small crabs (8% of overall diet). Clams and small crab were consumed more often in areas which had been inhabited for 10 to 30 years. The proportional discrepancy from the population level mean of green urchin consumed by sea otters demonstrated a clear trend of increased prevalence in the diet with decreasing persistence, akin to the pattern for red sea urchins (Figure 3.4).

Sea otter diet varied with exposure and persistence during our study period. The PerMANOVA analysis identified a two significant factors, exposure (*Pseudo-F* = 2.36, $p = 0.031$) and persistence (*Pseudo-F* = 1.93, $p = 0.046$) while the interactive term consisting of both persistence and exposure was not significant in determining prey composition in our study (*Pseudo-F* = 1.69, $p = 0.088$). Multivariate dispersion was assessed on the Bray Curtis dissimilarity matrix,

and no significant differences in multivariate spread were found for exposure ($F_{(2,14)} = 1.21$, $p = 0.327$) or persistence ($F_{(6,10)} = 0.651$, $p = 0.689$) providing support that a type-1 error is unlikely in our PerMANOVA analysis. The similarity percentage analysis (SIMPER) identified three commercial species including red sea urchins (21% contribution to similarity), sea cucumbers (12%), Dungeness crab (8 %), in addition to clams (10%) and green sea urchins (6%) as the main species driving similarities in the multivariate analysis, contributing to 57% of similarities within prey groupings.

Three well defined groups were identified in the nMDS analyses (2D stress = 17%; Figure 3.6) which supports our results from the PerMANOVA analysis. Based on the nMDS ordination, geoduck clam, red sea urchin and pinto abalone prey types were associated with exposed areas while Dungeness crab, California sea cucumber and urchin prey types were associated with protected areas. The least cost distance from release sites ($R^2 = 0.43$, $p = 0.031$) and latitude ($R^2 = 0.63$, $p = 0.010$) significantly fit the ordination and were strongly correlated with each other (*Pearson* $r = 0.84$, $p < 0.001$). Longitude, maximum density of sea otters and persistence were not identified as significant continuous variables.

Sea otter diet diversity (Shannon-Wiener H') increased log-linearly with sea otter persistence ($R^2 = 0.67$, $F_{(1,15)} = 31.8$, $p < 0.001$; Figure 3.7). The original translocation areas exhibited the greatest diet diversity, while areas that were only recently colonized had less diverse diets. Further, a demarcation was observed in the relationship of persistence and diet diversity. Areas which had been inhabited for less than 8.8 years and had a diet diversity index $H' < 1.2$ supported commercial invertebrate fisheries, while areas with a diet diversity index $H' > 1.2$

which had been inhabited by sea otters for greater than 9 years did not support commercial fisheries (Figure 3.7).

Discussion

The diet composition of the growing sea otter population in southern Southeast Alaska consisted of commercially important species when sea otters initially colonized unexploited habitat; diet diversity increased with duration of sea otter occupation. Red sea urchins and Dungeness crab were the most prevalent prey types in newly colonized areas in southern Southeast Alaska. Red sea urchins are a known preferred prey of sea otters and are often the first prey species targeted by sea otter after colonization (Ebert 1968, Hines and Pearse 1982, Laidre and Jameson 2006, Tinker et al. 2008). Red sea urchins provided the highest rate of biomass gain by prey species in our study (4.31 g min^{-1}; Figure 3.A-1). Our results suggest that once preferred prey is reduced, the population level diet of sea otters diversifies to include clams including geoduck clams, California sea cucumbers and small crabs, with the most diverse prey composition being found at sites occupied longest. Diet diversification is likely a result of two consequences of population growth in southern Southeast Alaska: (1) emigration to new habitat types, which support differing prey until those prey are depleted and (2) prey switching in areas colonized for an extended time. The diversification of diet as a function of persistence observed in our study is similar to results from other studies (Ostfeld 1982, Tinker et al. 2008). Prey quality is likely the primary factor in habitat selection by sea otters in the study area (Chapter 2). Considering all foraging regions in which data were collected, which vary in habitat type, sea otter persistence and density, we documented that in areas with 9 or more years of sea otter colonization commercial shellfisheries were no longer present and diet diversity increased (Figure 3.7). Two

commercially important species, pinto abalone and red king crab were found at low proportions in the diet of sea otters. Pinto abalone are a known preferred prey of sea otters (Watson 2000); however, in our study abalone were not an important prey source. Pinto abalone were overharvested in Southeast Alaska by commercial fishing in the 1980s and 1990s (Woodby et al. 2005), significantly reducing the population. A recent petition to list the species as endangered in 2014 provided evidence of significant depletion but was not supported for endangered listing by the National Marine Fisheries Service (Busch et al. 2014). The pinto abalone population in our study area is likely low enough where sea otters are present that encounters between the species are rare. Further, red king crab encounters by sea otters were very low as the protected bays with known concentrations of red king crab have yet to be colonized by sea otters in southern Southeast Alaska.

The correlated variables, latitude and least cost distance from release site, were factors associated with the diet composition of sea otters in southern Southeast Alaska. After sea otters were released in 1968 the pattern of recolonization followed a generally northerly trend along the outside coast and was likely a consequence of the availability of red sea urchin barrens on the rocky outside coast. Our PERMANOVA analysis identified exposure and persistence as important variables describing diet with red sea urchins, sea cumbers and Dungeness crab driving that result. Additionally, the nMDS ordination identified persistence as an important continuous variable (although not at the 95% level), which supports that sea otters diet consisted of both red and green urchins when first colonizing an area based on exposure, with green urchins associated with less exposed areas and red urchins with more exposed areas. As sea otters colonized further northward along Kuiu Island and began colonizing more protected

waters to the current distribution, the commercial component of the diet was dominated by Dungeness crab and California sea cucumbers. This is likely a consequence of different habitats being exploited by sea otters, because different habitats were associated with different prey species in our multivariate analysis. Further, several prey species are at or near their northern limit in southern Southeast Alaska including geoduck clams (Goodwin and Pease 1989, Harbo 1999), which may explain why sea otter diet was less likely to contain species such as geoducks as latitude and distance from release site increased.

The reintroduction of sea otters to southern Southeast Alaska is a conservation success story as positive growth has been observed since the population was established (Figure 3.2). However, many communities within the study area have expressed concerns over the impacts sea otters are having on the sustainability of commercial shellfisheries leading to proposed legislation targeted at reducing sea otter abundance (Carswell et al. 2015). Currently, the only known limitation to the growth of the sea otter population in the study area is subsistence harvest and density dependence in regions where sea otters have been established for 35 or more years (Chapter 2). The growth rate of sea otters (12% per year) in the study area is similar to other successfully reintroduced sea otter populations in Washington and British Columbia and has followed the same trend of slow growth after reintroduction, likely a result of a founder effect, followed by rapid growth approaching $R_{max,}$ and then gradual reduction in the growth rate to current levels ranging from 9% to 14% (Bodkin 2015, COSEWIC 2015, Laidre et al. 2009). Further, the 2-dimensional complex coastline of southern Southeast Alaska has led to a consistent expansion in the range of sea otter after an initial founder effect common in translocated populations (Hundertmark and Van Daele 2010, T.Tinker, USGS, personal communication 2014). A

substantial amount of habitat (41% of area with depths less than 60 m) has yet to be colonized by sea otters in southern Southeast Alaska (Figure 3.1). The population will likely continue to grow until as vast areas of red and green sea urchin barrens are present in southern Southeast Alaska (Hebert 2014) and the subsistence hunting rate is currently below the annual growth rate (Chapter 2). The square-root of area occupied (Figure 3.3) describes a diffusion process, where range expansion will continue until the population hits boundaries and decelerates. Therefore, deceleration is a function of boundary conditions, which appear to be minimal in Southeast Alaska's complex 2-dimensional coastline, in contrast to the California coastline, which is more 1-dimensional in nature and where sea otter range expansion appears limited by range boundaries (T. Tinker unpublished data).

The ecological consequences of sea otter predation have been well studied, and density dependence has been identified as a driver of population level diet diversification and is especially evident in rocky habitats (Newsome et al. 2015). The consequences of sea otter predation for soft sediment habitats are less understood but these habitats are likely more resilient to sea otters, as they have the ability to support higher densities of sea otters for longer times, and the prey associated with these habitats is likely less susceptible to predation (Weitzman 2013). We provide evidence that areas with the highest density of sea otters are associated with a low contribution of commercially important prey in sea otter diets. This result is likely a consequence of protected regions in southern Southeast Alaska that have predominantly clams as a prey source. Therefore, soft sediment communities will likely provide for the highest density of sea otters in southern Southeast Alaska, as has been observed in Glacier Bay, in northern Southeast Alaska (Weitzman 2013). Geoduck clams may be the single

existing shellfishery that could coexist with sea otters, although at reduced harvest levels compared to current levels. Through foraging data collection we observed that sea otters, typically males, took multiple dives often extending over more than three minutes to extract geoduck clams. Geoduck clams do not appear to be preferred by all segments of a sea otter population in southern Southeast Alaska as the proportional contribution to diets varied with persistence levels. The non-preference by sea otters for geoduck clams maybe due to the deep burrowing, energetically difficult extraction, and distribution to depths deeper than sea otters typically dive (McDonald et al. 2015).

This study provides evidence that sea otters prefer commercially important prey and are likely having immediate and long lasting impacts on commercially important invertebrates in southern Southeast Alaska. The diversity of sea otter diets, which increased as persistence increased, likely reflects an increase in the diversity of available prey in the ecosystem as observed in our study. Following the reduction in urchin barrens and geoduck clam beds, essentially representing monocultures, the benthic ecosystem became more diverse, providing a more diverse diet for sea otters. These nearshore habitats supporting diverse prey assemblages, although less productive by current economic infrastructures, could result in or represent stable productive ecosystem states suggested by ecological diversity-stability theory (Macarthur 1955, McCann 2000), however, the challenge will be to manage and sustainably exploit these stable ecosystem states. Sea otter population trends are likely an excellent indicator for determining nearshore ecological stability and should be closely monitored. The management of nearshore ecosystems, including fisheries within, can scarcely be made without considering sea otters. Our results are not surprising as preferred prey species are aligned with commercially important shellfish. We

predict that the sea otter population will continue to grow in numbers and distribution because preferred prey, as indicated by the presence of commercial fisheries, still occur in large areas which sea otters have yet to colonize or have just recently colonized. We suggest that sea otters be included in the management of existing or future nearshore fisheries, and that agencies responsible for the management of these species take an ecosystem perspective when setting harvest levels, for example including predation rates of sea otters on shellfish abundance or redefining sustainability in the presence of an apex predator. Finally, we suggest conducting long term studies on multiple species indirectly impacted by sea otters and suggest southern Southeast Alaska as an opportune place for these studies.

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Figures

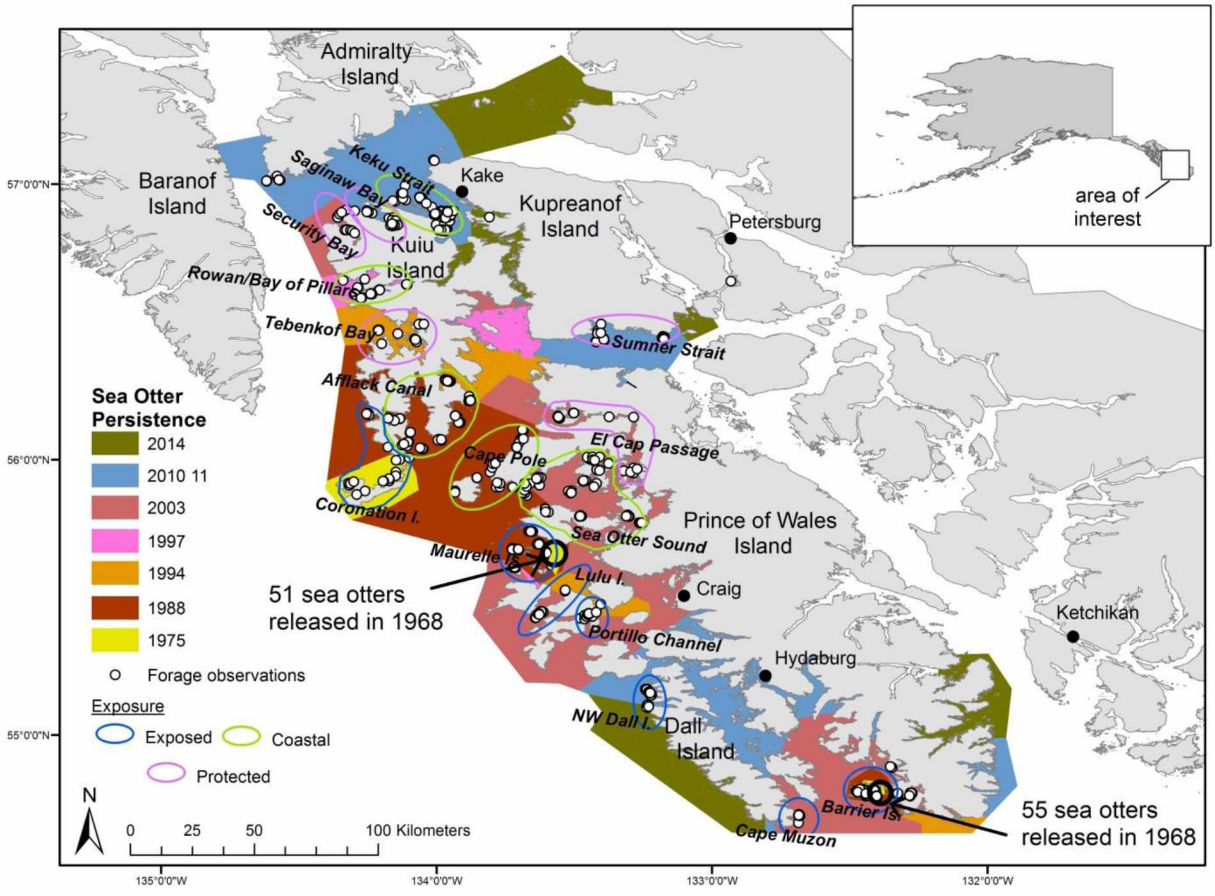

Figure 3.1 Distribution of sea otters in southern Southeast Alaska between 1975 and 2014. Release sites for 106 sea otters in 1968 are depicted as black circles and identified with arrows. Locations of forage observations collected between May 2010 and September 2012 and foraging regions in which forage observations were grouped are mapped using color-coded polygons representing the exposure at each region.

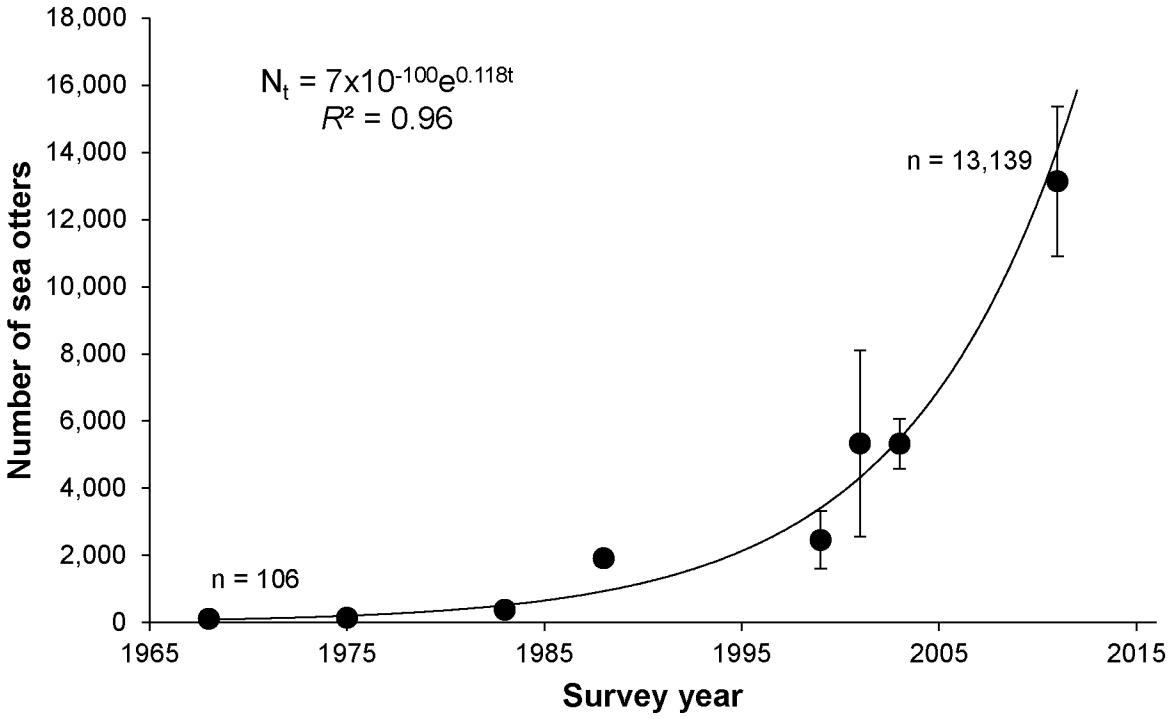

Figure 3.2 Trend in abundance of sea otters in southern Southeast Alaska between 1968 and 2010. One hundred and six sea otters where translocated to the study area in 1968 at two locations (Figure 3.1). Data are from seven sea otter population estimates conducted using a variety of methods. Error bars represent 95% confidence intervals. An exponential growth model was fit to available abundance estimates over time ($R^2 = 0.96$, $F(1,7) = 189.2$, $p < 0.001$). Data from Burris and McKnight (1973), Esslinger and Bodkin (2009), Hodges et al. (2008), Jameson (1989), Johnson et al. (1983), Schneider (1975), USFWS (2014).

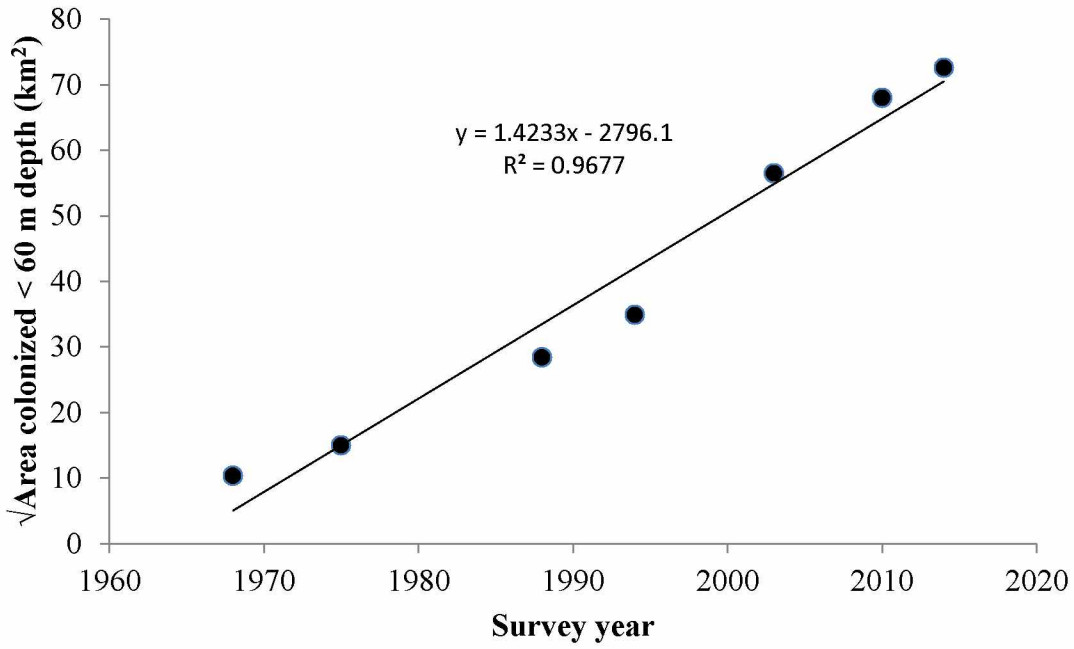

Figure 3.3 Square-root of area colonized by sea otters in southern Southeast Alaska calculated from distribution and assessment surveys conducted between 1975 and 2014. The x-axis represents the year. The y axis represents the square root of area less than 60 m in depth colonized by sea otters in the study area. The linear relationship between the two variables is plotted. The linear relationship ($R^2 = 0.97$, $F(1,5) = 43.0$, $p = 0.001$) suggests, assuming a sustained rate of growth is 12% and colonization occurs by a diffusion process, the radial rate of increase of the population is 1.42 km y^{-1} .

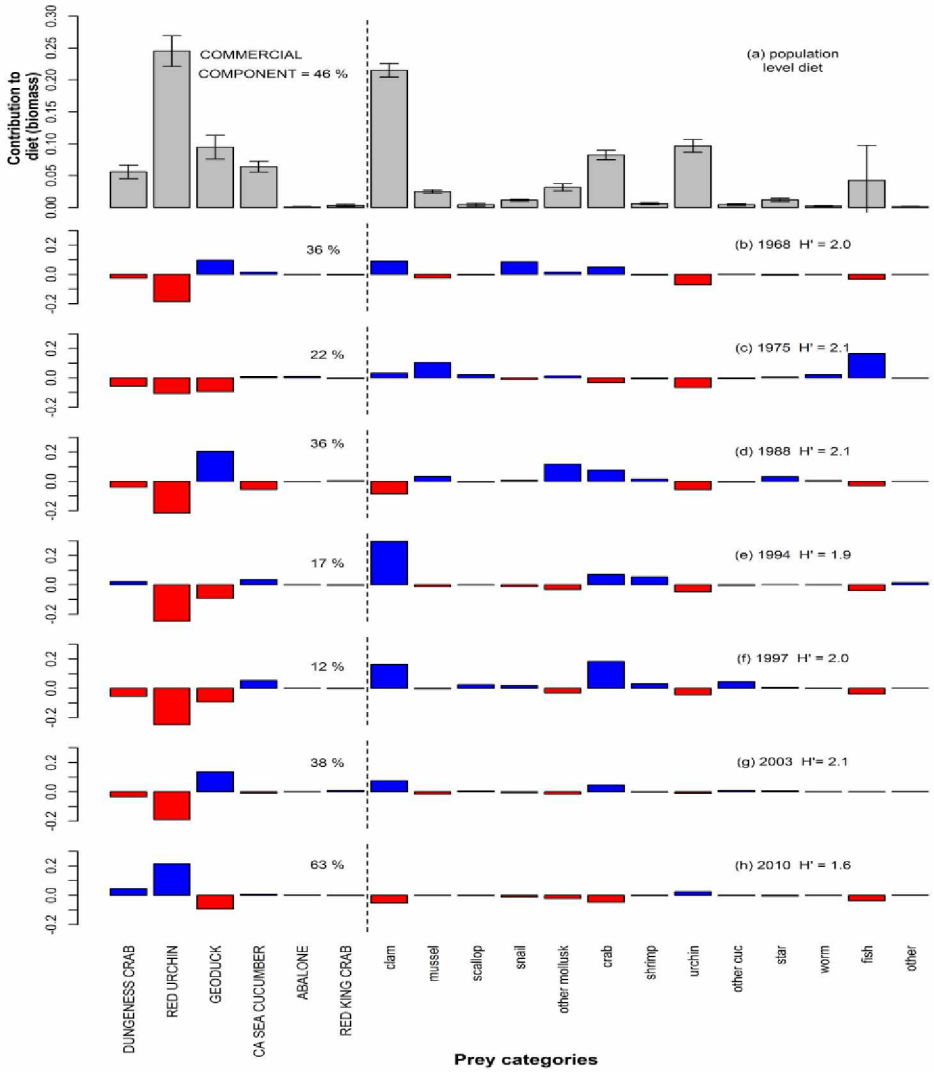

Figure 3.4 Diet composition in terms of (a) biomass consumed by sea otters in southern Southeast Alaska grouped into 19 categories (n = 7,587 forage dives. Error bars represent ± 1 SE. b-h) Proportional discrepancies of diet composition in edible biomass of 19 prey groupings from the overall population mean in (a) for increasing persistence levels (bottom to top). The year on each panel represents the persistence level of foraging observations. Commercially important species are represented by capital letters and the commercial component of the diet and the Shannon Wiener index (*H'*) are present for each persistence level.

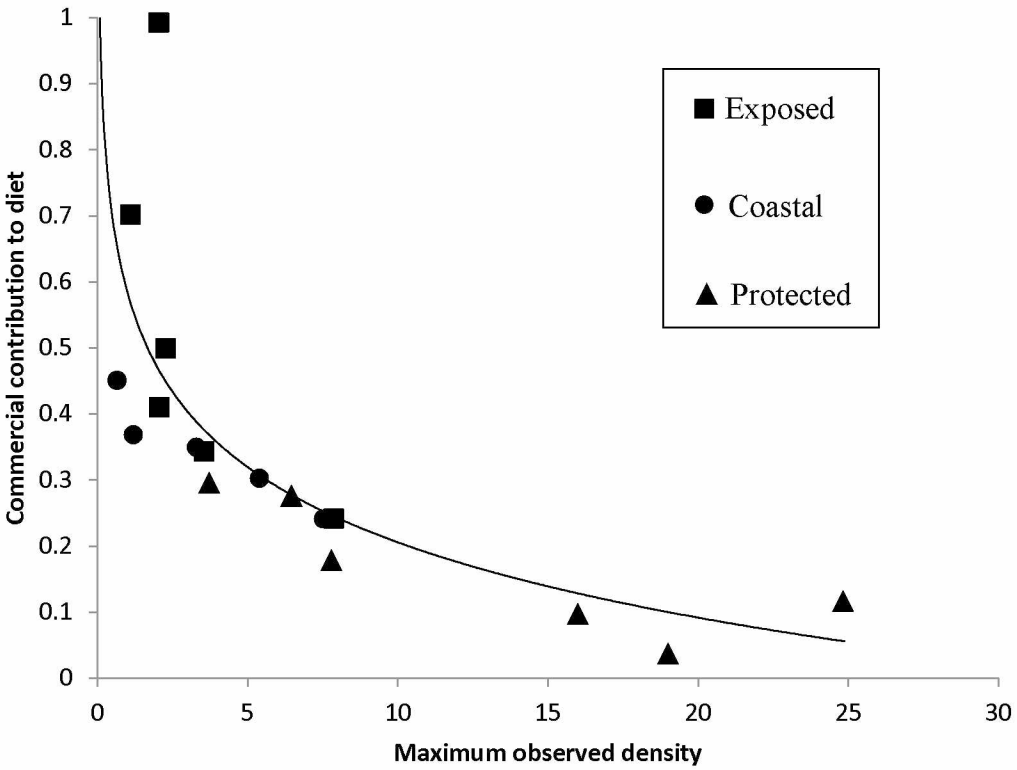

Figure 3.5 Commercial contributions to the diet of sea otters in southern Southeast Alaska as a log-linear function of the maximum observed density of sea otters at 17 foraging regions (R^2 = 0.45, $F_{(1,15)}$ = 12.5, p = 0.003). The exposure classification of each foraging region is depicted in Figure 3.1, and commercial prey species are presented in Figure 3.4.

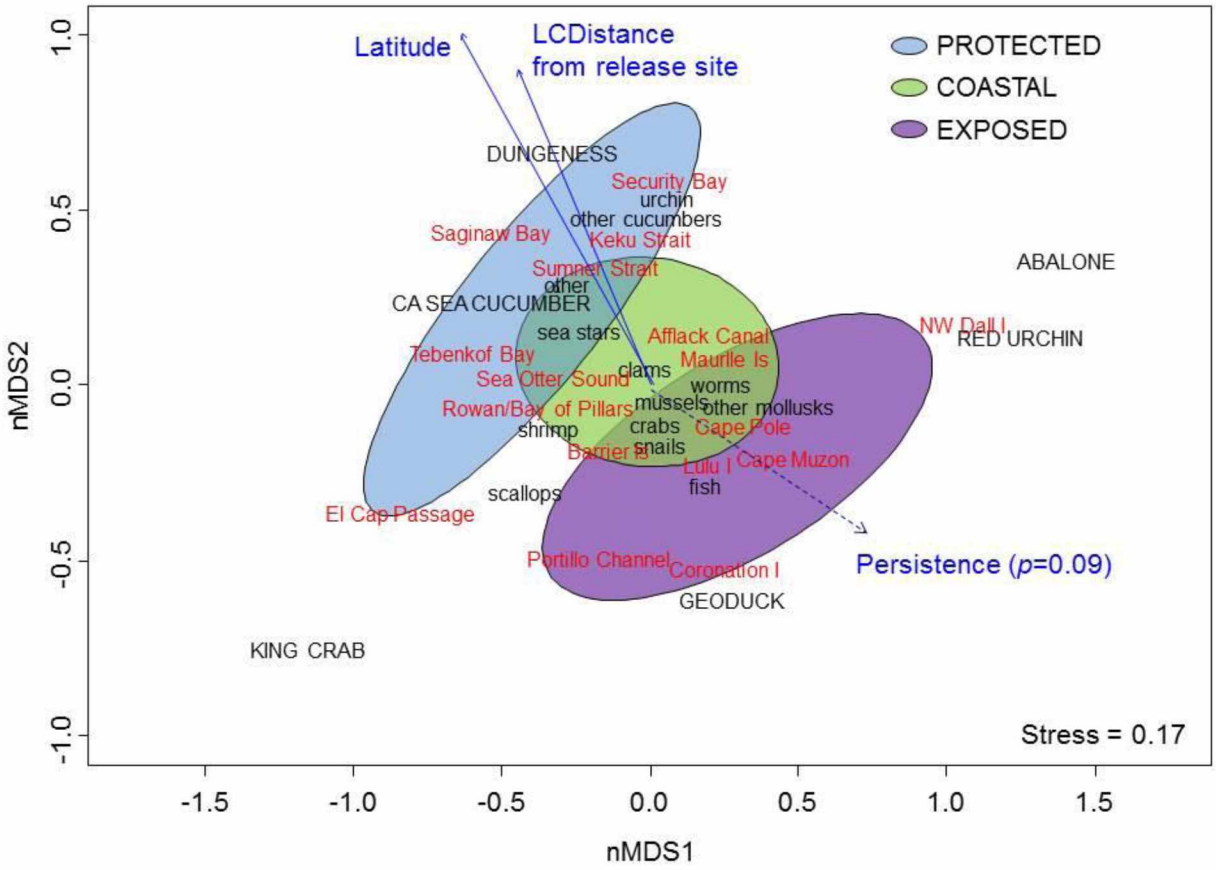

Figure 3.6 Plot of the first two axes from a nMDS ordination of 17 foraging regions and 19 prey groups (commercial important species in capital, site (red), prey groups (black)) in southern Southeast Alaska. Distances between two points reflect the dissimilarity in terms of prey composition. Significant continuous variables, determined by regression, include the least cost distance from release site and latitude and are plotted as blue vectors and significant categorical variables as ellipses defined by the legend, the non-significant variable persistence (p = 0.09), is plotted as a dashed blue line while longitude (p = 0.62) and maximum density of sea otters (p = 0.37) were omitted for clarity.

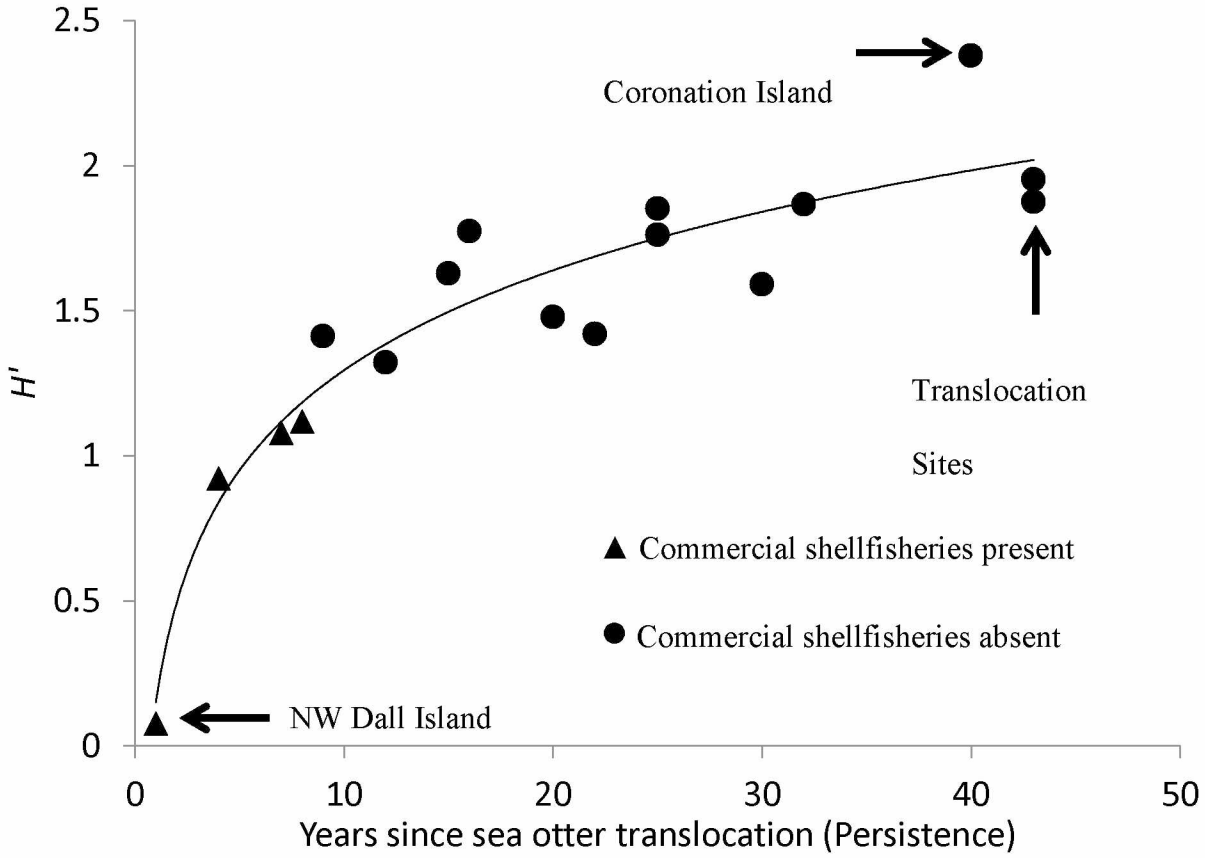

Figure 3.7 Shannon-Wiener's diversity index (*H'*) of observed prey as a log-linear function of sea otter persistence or years since sea otter translocation ($R^2 = 0.67$, $F_{(1,15)} = 31.8$, $p < 0.001$) at 17 foraging regions. Regions represented by triangles support commercial shellfisheries while regions represented by circles do not support commercial shellfisheries.

Appendix 3.A Supplemental material, population level biomass intake rate

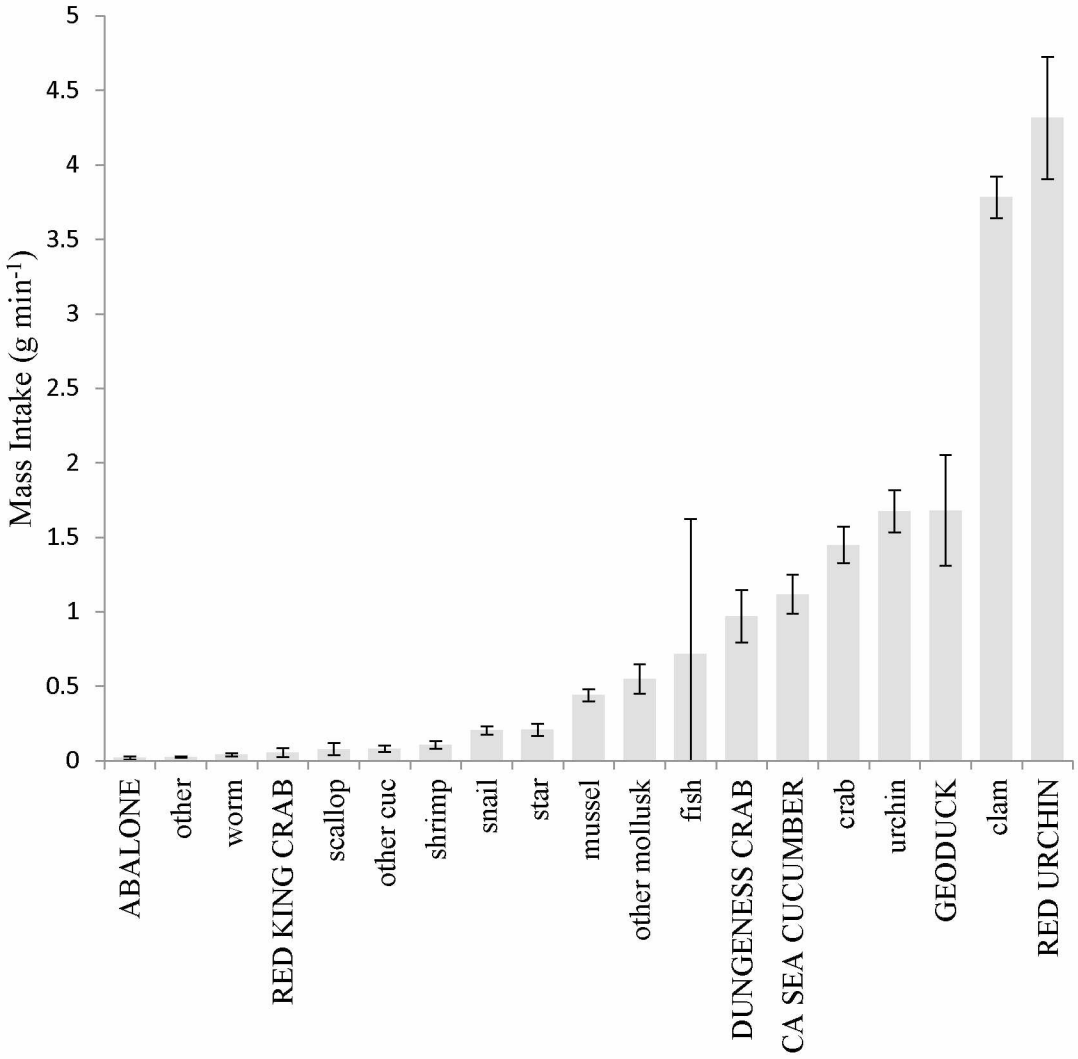

Figure 3.A-1 Biomass intake rate of sea otters determined from foraging observations in southern Southeast Alaska by prey grouping. The intake rate is calculated by the edible biomass (grams) consumed per minute of time spent by sea otters foraging including diving and prey processing time. Error bars represent 95% confidence intervals. Prey groupings in capital lettering represent commercial prey species.

General Conclusions

The reintroduction of sea otters to southern Southeast Alaska is a conservation success story. The sea otter population in southern Southeast Alaska grew from 106 individuals released at two locations in 1968 to an estimated 13,139 individuals in 2011. Although the population abundance has not been assessed since 2011, the distribution of the population continued to radiate between 2011 and 2014 at a similar rate experienced since reintroduction (1.42 km y^{-1}). However, limitations to the growth of sea otters were identified at one of the range edges between November 2012 and April 2014 as a result of increased subsistence harvest of sea otters. Subsistence harvest of sea otters increased substantially in Southeast Alaska during the 2012 reporting year; however, the number of sea otters harvested in the region did not limit sea otter growth. Additionally, areas where sea otters have persisted for > 35 years have become resource limited, as density estimates have decreased or stabilized and diet has diversified. No additional limitations to the southern Southeast Alaska population were identified. Approximately 41% of the potential habitat (area < 60 m in depth) has not been colonized by sea otters in southern Southeast Alaska, mostly in areas to the east of Prince of Wales and Kupreanof Island, characterized as being less exposed to the Gulf of Alaska. Therefore sea otters will likely continue to expand their range and increase in abundance.

The diet of sea otters was represented by 46% commercially important species between 2010 and 2013 in southern southeast Alaska. Commercial species, particularly red sea urchins and Dungeness crab, were initially targeted by sea otters when they colonized new unexploited

habitats. Sea cucumber and geoduck clams were consumed by sea otters in areas with varying persistence. Shrimp (*Pandalus spp.)*, pinto abalone (*Haliotis kamtschatkana*) and red king crab (*Paralithodes camtschaticus*) did not appear to be important food sources for sea otters in the study area. As the length of sea otter colonization increased the diet diversity of sea otter increased and the proportion of commercially important species decreased. Sea otters are known to forage optimally, meaning they will select prey items to maximize their energy intake rate (Ostfeld 1982). Urchins and clams provided the highest biomass intake rates for sea otters. This study described reductions in red sea urchin and geoduck clam abundance and Dungeness crab catch as a result of sea otter presence and implies economic losses to commercial fisherman and fishing communities as a result of sea otters.

Prior to the work presented here and Larson et al. (2013), evidence directly implicating sea otters in the decline or failure of various shellfisheries was poor due to limitations in sea otter abundance data, long term fisheries assessments, and sea otter forage data. Along the west coast it has been suggested that fisheries collapses resulted from a combination of sea otter impacts and unsustainable fishing practices (Estes and VanBlaricom 1985). However, this study provides evidence that in areas where sea otters are not present, the biomass or catch of commercially important shellfish appears stable in both fished areas and fishing reserves, suggesting that current harvest rates are sustainable. This warrants further investigation. Further this study was conducted in an area in which recreational fisheries and other human impacts, including pollution, are minimal or non-existent due to the low human population densities. Within the current range of sea otters in southern Southeast Alaska, sea otters outnumber humans (State of Alaska 2010, USFWS 2014). This work strongly implies sea otters are impacting commercial

shellfish fisheries in southern Southeast Alaska. This work also indicates that certain species are more susceptible to sea otter predation than others. This is likely due to life history characteristics, including mobility or habitat use (complexity) of individual prey species. For example sea urchins and abalone may be reduced to low levels by sea otters but can persist at lower abundances in habitats where refuges exist, i.e. cracks and crevices. Crustaceans are probably less vulnerable than clams and echinoderms (sea urchins and sea cucumbers) because they are more mobile and require visual cues for capture rather than the combination of tactile and visual cues. Additionally crustaceans, particularly larger crabs such as Dungeness crab and red king crab, likely have some refuge in deep water where sea otters cannot effectively forage (Scheding 2004).

Reduced densities of shellfish species to levels which are no longer commercially viable does not imply that these shellfish populations are at risk of extinction. Sea otters and their prey have coexisted in the North Pacific since the mid-Pleistocene epoch (Riedman and Estes 1990). However, commercial fisheries have only existed since sea otters were reduced to near extinction in the North Pacific Ocean. The abundance of certain macroinvertebrates in which commercial fisheries developed in Southeast Alaska is likely the result of sea otters being absent from the nearshore ecosystem from approximately 1850 until reintroduction in 1968 (Burris and McKnight 1973, Katrina Wessels, USFWS, personal communication, 2014). Many of these macroinvertebrates such as geoduck clams and red sea urchins are long lived broadcast spawners which may be characteristics that evolved with high predation (Ebert 2008, Vadopalas et al. 2011). In the absence of sea otters, dense beds of geoducks and urchin barrens likely resulted and these ecosystem states became accepted as "normal" by coastal communities that benefited

greatly from abundant and easily acquired shellfish resources. However, the productivity in terms of fisheries potential for ecosystems in which sea otters exist at or near equilibrium has not been realized and should be investigated.

Sea otters have been hailed as necessary and critical for maintaining ecosystem health and function in many marine systems, including kelp forests and eelgrass beds, but their role in nearshore ecosystems relating to commercial potential is not fully understood (Estes et al. 1989). Commercially important species such as herring and salmon, two of the largest and most lucrative commercial fisheries in Southeast Alaska, may benefit by ecosystem states with sea otters. For example, Pacific herring in Southeast Alaska spawn on many kelp species and eelgrass (Shelton et al. 2014), and future research should be conducted on the indirect impacts of sea otters on existing or potential new commercial fisheries. New research is especially critical in soft substrate and areas with glacial influence, which dominate the subtidal landscape in areas that sea otters have yet to colonize in Southeast Alaska.

Although undoubtedly sea otters have and will continue to impact the economies of Southeast Alaska, the economic benefit of sea otters realized through wildlife viewing, eco-tourism, and other, non-exploitive economic benefits need to be identified. Non exploitive benefits of sea otters in California were estimated at 3-16.4 million dollars annually and will likely increase as the California population of sea otters increases (Carswell et al. 2015, Loomis 2005). However, culturally, Alaskans differ remarkably from Californians and the economic benefits are likely different than those in California and should be investigated. The increase in sea otter populations in Southeast Alaska could provide for an increased "handicraft" market as Alaska

Natives have begun actively marketing "handicrafts" made from sea otter fur; however, uncertainty and vagueness of existing regulations are currently limiting the potential for economic growth of a sea otter handicraft industry. Further, if sea otter populations expand towards the community of Ketchikan, a large cruise ship port, new wildlife viewing opportunities could be available. The economic benefits to small coastal communities in which sea otters populations exist are possible and in addition to exploitive ventures, non-exploitive ventures such as ecotourism opportunities could mitigate the impacts to shellfisheries.

This study identified that coastal communities can limit the growth potential of sea otters. Aleut hunters are thought to have controlled sea otter populations based on midden records which depict two distinct and stable nearshore communities; one with dense sea otter populations and one without. This was likely a result of continuous exploitation by the indigenous communities (Simenstad et al. 1978). The translocation of sea otters rapidly accelerated the change from one stable state void of sea otters and dominated by epibentic herbivores and mesopredators to an alternate stable state in which sea otter predation maintains macroalgae and diverse soft sediment communities. This study provides evidence that two alternate stable states are possible in southern Southeast Alaska. Nearshore ecosystems could be managed for any number of goals through the management of an entire ecosystem rather that the current practice in which single species management predominantly focuses on the optimal use of a single species (Carpenter et al. 1999, Holling and Clark 1975, Levin 1999). These nearshore systems appear to be greatly influenced by top down forcing although bottom up control should be further studied, as nearly all early life history stages of sea otter prey are planktonic in nature and susceptible to numerous

environmental forces. Undoubtedly, the presence or absence of sea otters and sea otter predation needs to be incorporated into the management of nearshore systems in Southeast Alaska.

Finally, I hope this dissertation will stimulate future studies, particularly on the indirect impacts of sea otters on coastal ecosystems, and I suggest southern Southeast Alaska as an ideal place for these studies to occur. I hope the results presented here can provide information for resource managers, fisherman and coastal Native communities regarding changes that will continue to occur as a result of sea otter population growth and exploitation.

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Appendices

Appendix A

USFWS Marine Mammal Permit approval

DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE

3-201
(1/97)

FEDERAL FISH AND WILDLIFE PERMIT

1. PERMITTEE
MARINE MAMMALS MANAGEMENT
1011 E. TUDOR RD.
ANCHORAGE, AK 99503
U.S.A.

2. AUTHORITY-STATUTES
16 USC 1533 (d)
16 USC 1371 (a) (1)

REGULATIONS *(Attached)*
50 CFR 17.32
50 CFR 18.31

3. NUMBER
MA041309-4 AMENDMENT

4. RENEWABLE
☐ YES
☒ NO

5. MAY COPY
☐ YES
☒ NO

6. EFFECTIVE
03/07/2008

7. EXPIRES
03/06/2013

8. NAME AND TITLE OF PRINCIPAL OFFICER *(If #1 is a business)*
ROSA MEEHAN
CHIEF

9. TYPE OF PERMIT
MARINE MAMMAL/THREATENED SPECIES

10. LOCATION WHERE AUTHORIZED ACTIVITY MAY BE CONDUCTED
Coastal Alaska

11. CONDITIONS AND AUTHORIZATIONS:

A. GENERAL CONDITIONS SET OUT IN SUBPART D OF 50 CFR 13, AND SPECIFIC CONDITIONS CONTAINED IN FEDERAL REGULATIONS CITED IN BLOCK #2 ABOVE, ARE HEREBY MADE A PART OF THIS PERMIT. ALL ACTIVITIES AUTHORIZED HEREIN MUST BE CARRIED OUT IN ACCORD WITH AND FOR THE PURPOSES DESCRIBED IN THE APPLICATION SUBMITTED. CONTINUED VALIDITY, OR RENEWAL, OF THIS PERMIT IS SUBJECT TO COMPLETE AND TIMELY COMPLIANCE WITH ALL APPLICABLE CONDITIONS, INCLUDING THE FILING OF ALL REQUIRED INFORMATION AND REPORTS.

B. THE VALIDITY OF THIS PERMIT IS ALSO CONDITIONED UPON STRICT OBSERVANCE OF ALL APPLICABLE FOREIGN, STATE, LOCAL OR OTHER FEDERAL LAW.

C. VALID FOR USE BY PERMITTEE NAMED ABOVE.

D. Acceptance of this permit serves as evidence that the permittee understands and agrees to abide by the attached Special and General Permit Conditions.

E. Authorized to take for the purpose of scientific research up to 25,000 individuals per year of northern sea otter, (Enhydra lutris kenyoni) in Alaskan waters during aerial and/or boat skiff surveys, as described in application file and as conditioned below; up to 100 of these animals may be taken per year for capture, re-capture and release activities as described in application file and as conditioned below; an unlimited number of sea otter carcasses of both sexes and all age classes may be collected during beach surveys and necropsies performed as described in application file.

F. The permittee is authorized to take and release up to 100 per year northern sea otters (E. l. kenyoni) of all ages and sexes as follows: Capture, immobilize and hold, anesthetize, flipper tag, inject with subcutaneous PIT tag, collect morphometric and biological samples, including 1st premolar tooth, blood, fecal, urine, lesions, whiskers, skin punches (from flipper tagging procedure), and external swabs; a subset (up to 50 animals per year) consisting of adults and juveniles (both sexes but no pregnant females) may be captured/re-captured/transported (as per Conditions J & K) and abdomenally implanted with radio transmitters and time depth recorders (TDRs).

G. The Permittee is authorized to incidentally harass non-target sea otters, but harassment should be minimized as described in Permittee's application file. Every effort should be made to ensure that other marine mammal species are not in the immediate area prior to commencing authorized activity.

H. Should any marine mammal species other than northern sea otters be encountered during the authorized activities, Permittee must immediately move away from the site and detour around the animals, or if aerial, rise to over 1000 feet (305 meters).

I. Activities are limited to those conducted for the purposes, by the means, in the locations, and during the periods of time as described in the Permittee's application and supplemental information.

Conditions and Authorizations continue on page 2

☒ ADDITIONAL CONDITIONS AND AUTHORIZATIONS ALSO APPLY

12. REPORTING REQUIREMENTS
SUBMIT COMPLETE REPORT AS REQUIRED BY COND. R. TO DMA, 4401 N. FAIRFAX DRIVE RM. 212, ARLINGTON, VA 22203 BY 1/31 FOLLOWING EACH YEAR PERMIT IS IN EFFECT.

ISSUED BY
Susi J. Snethen

TITLE FOR
CHIEF, BRANCH OF PERMITS, DMA

DATE
03/07/2008

Appendix B

UAF IACUC approval

(907) 474-7800
(907) 474-5638 fax
fyiacuc@uaf.edu
www.uaf.edu/iacuc

Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 3, 2012

To: Ginny Eckert
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [195153-5] Sea otter recolonization and interactions with commercially important macroinvertebrates in southeast Alaska.

The IACUC reviewed and approved the Amendment/Modification to the Personnel List referenced above by Designated Member Review.

Received:	July 2, 2012
Approval Date:	July 3, 2012
Initial Approval Date:	April 15, 2011
Expiration Date:	April 15, 2013

This action is included on the July 26, 2012 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.

Appendix C

Approval from A. Rice for use of manuscripts in dissertation

presented as chapter 1 and 3 for this dissertation.

July 13th, 2015

To whom it may concern-

Zac Hoyt has my permission to use the following manuscripts as part of his thesis:

Reductions in commercially important macroinvertebrates associated with sea otters (*Enhydra lutris)* in Southeast Alaska

Hoyt, Z.H., G.L. Eckert, A. Rice, F. Mueter. Prepared for submission in Canadian Journal of Fisheries and Aquatic Sciences.

Recolonization and forage ecology of sea otters (*Enhydra lutris*) in southern Southeast Alaska

Hoyt, Z.N., M.T. Tinker, V.A. Gill, A. Rice, G. L. Eckert. Prepared for submission in Marine Ecology Progress Series.

Sunny (Allison) Rice

Sunny Rice
Alaska Sea Grant Marine Advisory Program
P.O. Box 1329
Petersburg, AK 99833
t: 907-772-3381
sunny.rice@alaska.edu

Appendix D

Approval from V. Gill for use of manuscripts in dissertation

presented as chapter 2 and 3 for this dissertation.

July 13th, 2015

Zac,

I give permission for you to publish these manuscripts as part of your thesis:

Chapter 2
Space use of northern sea otters (*Enhydra lutris kenyoni*) within an exploited and growing population[1]

---

[1] Hoyt, Z.N., G. L. Eckert, M.T. Tinker, V.A. Gill. Prepared for submission in Ecological Applications.

Chapter 3

Recolonization and forage ecology of sea otters (*Enhydra lutris*) in southern Southeast Alaska[1]

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[1] Hoyt, Z.N., M.T. Tinker, V.A. Gill, A. Rice, G. L. Eckert. Prepared for submission in Marine Ecology Progress Series.

Cheers, Verena

<><><>